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Ecology of asexual reproduction in hepatics

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Academic dissertation

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In honour of Dr. Hans Buch (1883-1964)

Dedicated to "pikku-i" Aino Lindberg

MOTTO:

"Tu ricavi solo segnacoli, indizi, per trarne la congettura che chiamiamo visione... E tra le molte certezze di cui lamentiamo l'assenza, una sola è presente, ed è il fatto che tutte le cose ci appaiono, e non è possibile che non sia verissimo che esse ci appaiono proprio così." Umberto Eco, *L'isola del giorno prima*

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List of original publications:

- I** Laaka-Lindberg, S., Hedderson, T.A.J. & Longton, R.E. 2000: Rarity and reproductive characters in the British Hepatic flora. - *Lindbergia* 25: 75-81.
- II** Laaka-Lindberg, S. 1999: Asexual reproduction in a population of *Lophozia silvicola* Buch in central Norway. - *Plant Ecology* 141: 137-144.
- III** Laaka-Lindberg, S. 2000: Substrate preference and reproduction in *Lophozia silvicola* (Hepaticopsida) in southern Finland. - *Annales Botanici Fennici* 37: 85-93.
- IV** Laaka-Lindberg, S. 2000: Biomass allocation to sexual and asexual reproduction in a leafy hepatic *Lophozia silvicola* Buch. - Accepted for publication in *Journal of Bryology*.
- V** Laaka-Lindberg, S. & Heino, M. 2000: Clonal dynamics and evolution of dormancy in the leafy hepatic *Lophozia silvicola*. - Submitted.

PROLOGUE

Bryological research has long honourable traditions in the University of Helsinki. However, ecology, evolution of life histories and reproductive biology of bryophytes has not received much attention either there or anywhere else. These subjects have been largely ignored by all except a few scattered individual researchers, and until recent times. In this respect the late hepaticologist Dr. Hans Buch was an exception. He placed emphasis on experimental work on reproductive biology, ecophysiology and taxonomy of hepatics. When reading his detailed, systematic observations on ontogeny of asexual propagules, one can only wonder, why has his work been so forgotten in the shade of his taxonomist colleagues'. Why haven't the questions how? and why? and how much? challenged anybody else familiar with these beautiful little plants? Reproductive ecology and evolution of life histories in bryophytes are still white spots on the map, and yet, he had seen it, he had written about it. Unfortunately he did not have the equipment and methods I have been able to use, and unfortunately for me, I have not been able to discuss my observations with him. Now, almost a century after Buch's doctoral thesis "Über die Brutorgane der Lebermoose", writing a thesis on asexual reproduction in hepatics brings me a strange dejavú: "Dr. Buch, I presume..."

1 INTRODUCTION

Reproductive traits are susceptible to natural selection. They evolve as a consequence of the environmental conditions in which organisms live, and are still affected by the ever changing world. Some traits are likely to be more central in facilitating adaptation to the environment than others. Today, in a world overwhelmingly ruled by human activities, the ability of a species to "behave adaptively" in fragmented natural habitats (Dettki et al. 1998, Higgins & Richardson 1999) becomes the corner-stone in its chances of avoiding extinction. Some people are worried about the survival of species and the protection of natural environments. International conventions and rules have been established to protect organisms and their habitats (e.g. IUCN Commission on National Parks and Protected Areas 1994), for example, the IUCN categories for threatened species (e.g. Mace & Stuart 1994). This classification uses quantitative, measurable criteria to emphasize the need for protective acts (Mace & Stuart 1994). Unfortunately, the criteria were originally based on threatened species such as the rhinoceros of the African savannahs rather than small, specialized organisms like epixylic hepatics that have complicated life cycles and occur in colonies with a clonal nature. Adjustments have been suggested (e.g. Hallingbäck et al. 1998) to better apply the criteria in order to cover plants and other "difficult" organisms. However, the central problem in applying the criteria has been a lack of knowledge, quantitative data, and of methods to measure the essential traits required to obtain the data. This lack of knowledge can be seen as the starting point to my studies on the reproductive ecology of hepatics, although the social motivation is shadowed by an honest interest in the subject.

Reproduction is one of the essential features of life, common to all living organisms in its various forms. For the definition of *reproduction*, I follow Mishler's (1988, 294) view as "production of a new, physiologically independent plant", completed by Mogie's (1992, 10) view of reproduction as an "event, which initiates a recapitulation of ontogeny". Modes of reproduction are numerous, ranging from the simple division of cells to complicated systems incorporating several stages within a reproductive cycle. Each stage experiences evolutionary pressures that produce a vast diversity in details. Reproduction is either *sexual* with haploid gametes merging in fertilization, combined with interchange of genetic information in recombination, or *asexual* with basically mitotic cell divisions transmitting identical genetic material from a parent to its progeny (Mishler 1988), these cells functioning as zygote equivalents (Mogie 1992). In clonal plants, including most of the bryophytes, it is important to recognize the difference between asexual reproduction and vegetative growth by undifferentiated regeneration from gametophyte fragments and by branching, even though the limit between growth and reproduction is not always clear.

Asexual reproduction is a significant adaptation to specific environments and biological conditions where the cost of sexual reproduction to a species is disadvantageous (Green & Noakes 1995, see also Schuster 1988). Asexuality can be seen as the reverse side of the coin "why sex?", which has been questioned among scientists over the history of biology (Ghiselin 1988). According to Ghiselin (*ibid.*), the question should be directed primarily to the genetic consequences of sex. In this study, however, I prefer Ghiselin's secondary definitions of sex, referring to fertilization and to differentiation of individuals into males and females, as the primary meaning of sex in

an ecological sense (see also Mishler 1988, Green & Noakes 1995). Awareness of the genetic consequences of reproductive modes forms the basis of the background to the evolutionary approach.

1.1. Asexual reproduction in hepatics

Asexual reproduction is very common among hepatics. Almost half of the species (46 %) in the British hepatic flora, at least occasionally, produce asexual propagules (I). In contrast, only 18 % of the species in the British moss flora produce some form of specialized asexual propagules (Longton & Schuster 1983, Longton 1992). Schuster (1988) discusses adaptational significance of asexual propagation in connection to its occurrence among species in contrasting climatic regions. Frequency and diversity of forms of asexual propagation are notably fewer in the tropics than in arctic and alpine areas (Schuster 1988).

The exclusive occurrence of asexual reproduction in the gametophytic phase in the life cycle found of bryophytes is unique among terrestrial plants (Wyatt 1994). The basis for the production and ontogeny of asexual propagules in bryophytes is given in thorough studies on mosses by Correns (1899), and on hepatics by Buch (1911) and Degenkolbe (1938). Regeneration from gametophyte fragments is perhaps the most common form of multiplication in mosses (Longton & Miles 1982), but is exceptional in hepatics (Longton & Schuster 1983). Several different types of non-sexually produced propagules, including gemmae, caducous leaves and shoots and tubers are found among hepatics. However, some of the forms formerly classified as "asexual" propagules do not meet the criteria of asexuality (see Mogie 1992) but merely represent different forms of vegetative growth. The development of asexual gemmae from specialized mother cells on the edges of the upper leaves of shoots in leafy hepatics is described and illustrated in Buch (1911). He provides evidence for the interpretation of gemmae as zygote equivalents sensu Mogie (1992). Buch (1911, see also Degenkolbe 1938) states that a certain developmental stage in tissues is required before gemma mother cells are sufficiently mature to divide and start functioning. Subsequently, these mother cells are not able to divide indefinitely, but only for a specific period (Buch 1911). In hepatics, vegetative growth is commonly facilitated by the branching of mature plants (Longton & Schuster 1983), which successively form large clones. In asexually reproducing hepatics, physiologically independent "individual" shoots are genetically identical to their mother plants. Therefore, stands of gemmiferous hepatics are clonal, even though shoots are not interconnected, representing an exceptional form of clonality among plants (see Klimeš et al. 1997).

1.2. Ecology and evolutionary significance of asexual reproduction

Characteristically, habitats and populations of bryophytes are patchily distributed (Söderström 1994, Söderström & Herben 1997). Therefore, population structure and dynamics are important to the long-term survival of a species in an area (Söderström 1994). Predictability of the environment, and spatial distribution of suitable substrate patches determine the adaptive reproductive strategy of the species. In an ecological framework, asexual reproduction can be seen as an effective way to enlarge and

maintain populations (Crow 1994), especially in marginal habitats (see e.g. Mishler 1988). Indeed, asexual propagation and vegetative growth in hepatics have been considered as "of paramount importance" to the survival of populations under marginal conditions (Longton & Schuster 1983, see also Kimmerer 1991b), but surprisingly, practically no experimental data is available. However, in many studies, asexuality has been considered as adaptive in stable environments (e.g. Charlesworth 1993) or in habitats with minimal biotic interactions (*r*-selection, see Mishler 1988), and phylogenetically, asexual species are considered as short-lived offshoots of originally sexual lineages (Crow 1994, see also Smith 1978). However, recent studies on stable environments show that survival is possible through the mere maintenance of populations, but in dynamic environments reproduction with successive dispersal of progeny is necessary (Söderström 1994, see also Schuster 1988). Furthermore, in temporally and spatially variable environments, dispersal and developmental delay such as dormancy are alternative adaptive strategies (McPeck & Kalisz 1998).

At first glance, the aforementioned views may seem quite opposite. Sex is not necessary for reproduction (Ghiselin 1988, Mogie 1992). Energetic, genetic and ecological cost of sexual reproduction is generally shown to be high (e.g. Crow 1994), and in studies on allocation to vegetative growth and reproduction for instance in vascular plants, multiplication without sex has been shown as an effective way to maintain local populations even against the risk of loss of genetic variation (Klekowski 1997, McLellan et al. 1997). Indeed, in certain situations, the asexual mode of reproduction may outweigh the advantages of sexual reproduction (see Crow 1994). Relevant characteristics of asexual reproduction in leafy hepatics with haplodiplontic life cycles and predominant gametophytic phase are that 1) asexual reproduction is often more effective (see Kimmerer 1991b) and less error-prone (Crow 1988) since in haploid organisms deleterious genes are immediately eliminated (Smith 1978, Wyatt 1994), 2) sporophytically expressed genes may be inactive in the gametophytic phase (Mishler 1988), and 3) the cost of asexual reproduction is less than of sexual reproduction (Crow 1994). Furthermore, Newton & Mishler (1994) have argued that as a consequence of the apical cell mode of growth in bryophytes, somatic mutations in asexual lineages provide levels of variation comparative to those in sexual lineages (see also Mishler 1988).

Green & Noakes (1995) have proposed an opportunistic strategy, involving asexuality with occasional sexual reproduction, by which advantages of both reproductive modes are obtained (see also McLellan et al. 1997). Occasional or facultative sexual reproduction is characteristic of many asexually reproducing bryophyte species. Facultative modes of reproduction may play different roles in ecology and evolution (Newton & Mishler 1994). Asexual propagules can be produced under more stressful conditions (Longton & Schuster 1983, Newton & Mishler 1994), and spores and asexual propagules disperse on different scales (Schuster 1988, Söderström & Herben 1997, see also Miles & Longton 1990). Drawing together the elements of Green & Noakes (1995) and Newton & Miles' (1994) discussion on the different roles of sexual and asexual reproduction (see also Söderström 1994) provides the theoretical framework, within which I address the questions concerning the role of asexual reproduction in hepatics, using a leafy species *Lophozia silvicola* Buch as a model organism.

1.3. The aims of this thesis

In this thesis I attempt to demonstrate evidence for the ecological and evolutionary significance of asexual reproduction in leafy hepatics. My basic questions are: 1) what is the role of asexual propagation in the formation of general distribution patterns in hepatics? 2) How can the production of asexual propagules be quantified? 3) Do the reproductive modes, whether sexual or asexual, have different energy costs? 4) Is the reproductive mode connected to environmental variables such as substrate quality and the spatial distribution of colonies? 5) How can the effectiveness of colonisation by asexual propagules be measured? 6) Is dormancy in asexual propagules an adaptive strategy, and if so, in what conditions? I have approached the questions from different angles in the five separate studies listed on page 4 and referred to by their roman numerals I-V.

The relationship between reproductive characters and general distribution patterns of hepatic species in British hepatic flora is analysed in paper I, which constitutes the background for studies on a model species *Lophozia silvicola* in papers II - V. A method for quantifying presence of asexual propagules on shoots in *Lophozia* is described in paper II, and further applied in papers IV and V. The phenology of production of asexual propagules in *L. silvicola* is reported in paper II from a locality in central Norway, and in paper V from a study area in southern Finland. A method to test germinability of asexual propagules through the growth season is described in paper II, and further applied in paper V. The relation between sexual and asexual reproduction in *L. silvicola* is studied in paper IV on the basis of allocation hypothesis. The frequency of asexual and sexual reproduction on different substrate types is examined in paper III. The population dynamic role and evolutionary significance of dormancy in asexual propagules is simulated and discussed in paper V.

2 MATERIAL AND METHODS

2.1. Terminology

Some discrepancies in terminology occur between the original papers and the thesis synopsis. In this chapter, the preferred definitions for the central concepts are given. In most cases, the outcome of the concept discrepancies is negligible since the meaning is circumstantially derivative. In this synopsis, however, the following terminology is consistently applied.

In bryophytes, *gametophytic* and *sporophytic* life stages are clearly heteromorphic, sexual reproduction occurring during the gametophytic stage (Wyatt 1994) with two *sexes*, *males* and *females*.

Sexuality refers to *monoicy* or *dioicy* of the species. Parallel terms *monoecious* and *dioecious* (paper I) refer accurately to sporophytes of higher plants, for which reason Mishler (1988, see also Wyatt & Anderson 1984) recommends use of *monoicy* and *dioicy* on bryophyte gametophytes, which is followed here.

Sexual morphs (IV) refer to the expression of sex on *Lophozia silvicola* shoots. *Females* are shoots with archegonia, and *males* are shoots with antheridia. Shoots, on which sex is not expressed are called non-gametangia-bearing, abbreviated as NGB. In paper IV, asexual shoots refer to NGB shoots. Non-gametangia-bearing shoots reproduce *asexually*, by means of *asexual propagules*, the *gemmae*. Colonies, in which *sexual reproduction* has occurred on the basis of fertilized archegonia being present, are called *fertile*. Colonies with female and male shoots are called *unisexual* or *bisexual* depending on the presence of one or both sexes.

In *sexual reproduction* in bryophytes, haploid gametes merge in fertilization and a diploid sporophyte develops (Mishler 1988). The exact meaning of *asexual reproduction* in hepatics refers only to the formation of propagules which develop from individual mother-cells on the gametophyte, germinate and develop in a pattern analogous to that of a germinating spore, and function as a *zygote equivalent* (see Mogie 1992). These criteria are met by the gemmae of *Lophozia silvicola* (see also Buch 1911), but unfortunately not uniformly by all propagules considered "asexual", for instance in paper I. Therefore, in this connection, the functional approach is applied for "asexual propagules" as a substitution of sexual reproduction by spores.

2.2. Studied species

In paper I, commonness or rarity among the 284 species of British hepatic flora are analysed on the basis of species occurrences in more than 2400 10 km British National Grid squares (Hill et al. 1991) in connection to frequency of sexual and asexual reproduction reported in literature (Smith 1990, Hill et al. 1991). In other papers (II-V) a boreal forest species *Lophozia silvicola* is selected as a test organism for more detailed studies on the significance of asexual reproduction.

Lophozia silvicola Buch belongs to the large, variable genus *Lophozia*, section *Lophozia* (see Schuster 1969), in the order of leafy hepatics, Jungermanniales, Hepaticopsida. The taxonomic status of the species is unsettled. However, in the boreal forests of northwestern Europe *L. silvicola* is recognizable, possessing a relatively constant range of morphologies separable from related taxa. A taxonomic treatment of *L. silvicola*, especially concerning nomenclatural interpretations, is in preparation. In order to avoid confusion, I follow Buch's definition in Herzog et al. (1933) and Buch (1942).

Lophozia silvicola has a wide circumboreal distribution in the conifer forest zone, with occurrences in alpine areas further south, and also in regions of the Arctic (see *Lophozia ventricosa* var. *silvicola* in Schuster 1969). It grows in closed, old-growth conifer forests, often in slightly marshy areas, as it requires a humid microclimate. *L. silvicola* grows frequently on decaying wood, but also on rock, moist humus or mineral soil, and occasionally on peat (Schuster 1969).

Lophozia silvicola is dioicous and exhibits a facultative mode of reproduction, either sexual or asexual. Asexual propagules, in the form of (uni-)bicellular gemmae, are produced at the tips of uppermost leaves (Figure 1 in paper II, see also Buch 1911). In

the study area in southern Finland, sexual reproduction occurs in about 16 % of the colonies of *L. silvicola*, but mostly relies on asexual reproduction. Colonies also spread vegetatively by branching.

2.3. Study areas

In paper I, the study area for the British hepatic flora is incorporated within the British National Grid system, i.e. England, Wales, Scotland and the main Channel Islands.

Material for paper II, on asexual reproduction and colonisation efficiency in *L. silvicola*, was collected in a lowland forest locality on the outskirts of the city of Trondheim, province of Sør Trøndelag, central Norway (10°11' E, 63°25' N). The locality is a spruce-dominated old-growth forest along a brook ravine at an altitude of 250 m a.s.l. The old-growth forest patch was surrounded by clear-cuts, and the vegetation was somewhat disturbed by sheep-grazing (see paper II).

Material for papers III - V was collected from Kotinen Nature Reserve in Lammi commune, South Häme, southern Finland (61° 14' N 25° 03' E). Kotinen Nature Reserve is representative of the primeval old-growth conifer forests of southern Finland, incorporating slightly marshy areas beside brooklets, and large amounts of decaying wood. The climatic conditions and vegetation of the Kotinen area are described in Bergström et al. (1995). *L. silvicola* is common in the area.

2.4. Counting the number of gemmae

The number of gemmae present on shoots were counted by scraping them into a drop of water on a microscope slide with a fine dissecting needle (II, IV, V). For each count, 10 individual shoots were systematically picked in a 1 cm² sample square under a glass frame: two shoots in the middle of each of the frames, and two in the center of the square. The gemmae were rinsed into 5 ml of distilled water in a class tube. A drop of mild detergent was added to prevent surface tension. The tube was then stirred in Vortex for 15 seconds to break up the clumps of gemma.

A drop of solution with gemmae was placed on haemocytometer (Fuchs-Rosenthal 0.200 mm), and the number of gemmae counted under a microscope at 40x magnification. Although basic counting gives the numbers of gemmae present per shoot, if the shoot density and the average colony area are known, the method also allows the extrapolation of the number per colony, and per colony area. For each sample, three haemocytometer fields are counted (II and V), except 10 for each sexual morph in paper IV.

The numbers of gemmae present on shoots were counted six times at intervals of one month, beginning from the snowmelt in mid-May to snowfall in mid-October. In paper II, the result is based on the growing-season of 1994, and in paper V, on a period of three years, from 1997 to 1999. In paper IV, numbers of gemmae were counted in samples of 50 shoots of the three sexual morphs collected in mid-summer 1997.

2.5. Testing germinability of gemmae

A liquid culture method (II, V) was applied and developed for testing germination and viability of the gemmae. This test gives an estimate of the potential for germination and for viability of the propagules, rather than a measure for actual germinability or establishment in natural conditions. The gemmae were scraped from the shoots similarly as for counting (Chapter 2.4.), but into a drop of liquid culture medium. Knop's solution was selected as the culture medium, following the recipe given in Nehira (1988). This medium is nearly neutral, inexpensive and preserves well. The Knop's solution was sterilized in an autoclave and preserved in sealed containers at room temperature.

The gemmae were rinsed into 10 ml of culture medium on Ø 6 cm petri dishes. The dishes were sealed with Parafilm in order to prevent evaporation and contamination, then placed on a white plate in diffuse light at room temperature (about 22°C). The temperature was kept as constant as possible. The light regime was set up to simulate the natural long-day conditions. The rate of germination was recorded after two (II) or three (V) weeks. A haemocytometer grid was used to avoid confusion in counting the germinated gemmae. In paper II, at least 100 gemmae were counted for each sample. In paper V, three countings of at least 30 gemmae were recorded for each sample.

A gemma was considered to have germinated, if its walls were notably swollen, and/or if a few-celled protonemal tube had emerged (see Figure 1 in paper II). Germination of gemmae proceeds slowly (Knoop 1984), hence at least two weeks incubation time were required (II, V). According to some author's (see Knoop 1984), the swelling of the propagule cell walls is caused by mere absorption. In paper V, to ensure reliable interpretation of the germination, the incubation time was extended to three weeks. Of the non-germinated gemmae, those with intact walls and coloured cell contents were considered as living and entering dormancy, and those with broken walls, discoloured cell contents, and shrunken protoplasm as dead (paper V).

2.6. Biomass allocation and the effect of shoot density

Allocation of biomass (IV) to sexual reproductive organs was measured by weighing (dry weight, µg). Fifty individual shoots of each sexual morph (non-gametangia-bearing (NGB), female and male) were randomly picked from a mixed colony. The shoots were left to dry in paper bags at room temperature for at least one week. Total dry weight of NGB, female and male shoots, and dry weight of sex organs were weighed by Cahn Model 4700 Automatic Electrobalance microweigh. Dried shoots are very light, indeed. Even in the microweigh, they had to be weighed in groups of 7-10 shoots. The number of these groups were used in a statistical test to establish differences in dry weight instead of the total number of shoots measured. The effect of sexual reproduction is also estimated by measuring the length of the shoots and branches, and by comparing branching frequency and pattern (see Fig. 1 in IV).

In papers II and V shoot density per colony area was measured by counting (n=3 for each sample) the numbers of individual shoots on a 1 cm² glass frame. In paper V,

shoot density in the sampled colonies was measured as a control for the effect of repeated sampling in the colonies. As no change in shoot density is detected, it can be concluded that the sampling itself does not significantly affect colony dynamics.

2.7. Substrate preference and colonization efficiency

The substrate preference (II, III) was based on the frequency of occurrences, and sexuality of the colonies on different substrate types. *Lophozia silvicola* grows on decaying logs and stumps, fallen branches and twigs, and pieces of wood on soil. All of these substrates were simply considered as wood. Colonies on a mixture of mineral and humus soil were considered to be growing on soil, and colonies on bare rock surfaces, usually on vertical walls of boulders, were considered as growing on rock.

Colonization efficiency (II) was estimated by comparing the frequency and surface area of colonies present to the numbers of available colony patches and area of free colonizable substrate in a study plot of 10x20 m. Frequency of occupied patches gave an estimate of local dispersal ability, and colony area an estimate of the success of establishment (II).

2.8. Modelling evolution of gemma dormancy

In paper V an individual-based cellular automata model (Judson 1994, Solé & Bascompte 1998) was used to test the adaptiveness of dormancy in the population dynamics in *Lophozia silvicola*. An individual-based spatial model was used (V) as it combines stochastic population events and spatial distribution of individuals (Judson 1994, Keeling & Rand 1995, Solé & Bascompte 1998) in a robust model, that was relatively insensitive to variability within the parameters. Thus, parameters estimated on the basis of highly variable real data still gave a realistic result. Finally, the model's predictions were tested against these real data, to see whether the evolution of dormant asexual propagules has prerequisites for existence in nature.

A model was constructed in order to examine the apparent decrease (paper II) in germinability of gemmae during the growing season. It was hypothesized that the non-germinating gemmae enter dormancy. The germinability schedule was the evolving strategy in the model, which was constructed on the basis of the field data available. Model simulations were set to run for 1000 years, during which the population evolved to a stochastic equilibrium. The last 200 years of the simulation were used to calculate mean population strategy and referred to as an evolved germination schedule. See paper V for a description of the model structure.

Parameterisation of the model (V) was based whenever possible on real population parameters as measured in the colonies of *Lophozia silvicola* at Kotinen Nature Reserve. Some estimates were difficult to obtain, e.g. real numbers of gemmae produced or released at each time interval, and thus feasible approximations were used instead (V). Estimates of the age at which individual shoots first produce asexual propagules, were based on experienced observations and circumstantial evidence rather than exact measurements. However, through model construction, it became obvious,

that changes in the parameter values complicated the model and extended the simulation times, but did not affect the general pattern of simulation results (see also Keeling & Rand 1995).

Model parameters included the following real data estimates:

- a. mean germinability of gemmae through the growth season measured over a period of three years (see Chapter 2.4.)
- b. survival of non-germinated gemmae estimated from the data of one growth season (1999) as the proportion of living non-germinated gemmae (see Chapter 2.4.)
- c. survival of shoots over winter, extrapolated from the proportion of shoots alive in the first sampling period in May
- d. survival of shoots through the growing season, as a geometric average from June to October over two years 1998-99
- e. average of total numbers of gemmae present on shoots over a period of three years.

In addition, monthly estimates of numbers of gemmae released were calculated from the real data by integrating the equation $dN(t)/dt = at(t-5.5) - cN(t)$, where N is the number of gemmae present, t is time in months starting from the beginning of the growing season, a is a parameter for the parabolic function for gemma production, and c is the disappearance rate of the gemmae (V). The resulting equation was then fitted to real data by non-linear regression.

2.9. Statistical analyses

Contingency analyses of two-way frequency tables were used to test associations between the traits in paper I. The null-hypothesis of independence in each of the two-way tables defined by various combinations of the trait categories were tested by G-statistics (I). In other papers, testing normality of the traits measured (Kolmogorov-Smirnov test with Lilliefors probabilities) did not allow use of parametric tests. Thus, non-parametric Kruskal-Wallis one-way ANOVA was applied (papers II, III, IV), with adjustment for unequal sample size (paper III, Zar 1984). Spearman's rank correlation test was applied in paper II for testing the correlation between shoot density and gemma production in the colonies. In paper III, χ^2 goodness-of-fit tests were applied in comparisons of observed against predicted frequency distributions of occurrences on different substrates.) In paper III one-tailed nearest-neighbour analysis with corrections for edge-effect and reciprocal pairs were applied for analysing spatial distribution of colonies (Campbell 1996. The Mann-Whitney U-test was applied in testing differences in average measures of the vegetative traits and numbers of gemmae present on shoots between the sexual morphs in paper IV. For the significance of the seasonal trend in numbers of gemmae present, ANOVA with repeated measures design adjusted by Huynh-Feldt statistics was applied (II, V). In paper V, a linear regression model was applied for testing the significance of the decreasing trend in germinability, and non-linear regression models in parameterisation for the cellular automata model. The tests were computed mainly by SYSTAT statistical software (Kirby 1993).

3 RESULTS AND DISCUSSION

3.1. Role of asexual propagation in the general distribution of hepatic species

In paper I, we investigated the relationships of general distribution patterns, reproductive traits, including sexuality, whether monoicous or dioicous, frequency of sporophyte production corresponding to sexual reproduction, and frequency of asexual propagation. All these characters have different effects on intraspecific characters determining the species dispersal ability and adaptive potential by means of genetic differentiation and gene flow. As was found to be the case in British mosses by Longton (1992), reproductive characters in hepatics are related to the likelihood of rarity (see also Higgins & Richardson 1999). Firstly, species which do not produce sporophytes are much more likely to be rare than those with frequent sporophyte production (I). This result is in agreement with previous studies (Miles & Longton 1990, Söderström 1992) that have considered spores to be the main means of dispersal. Secondly, monoicous species produce sporophytes much more frequently than dioicous species (I). Sexual reproduction in bryophytes involves motile sperms dependent on presence of water for facilitating fertilization. The distance between female and male gametangia is obviously a restricting factor (Longton & Schuster 1983, Wyatt & Anderson 1984, Longton 1990). In marginal habitats with severe weather conditions, very short range sperm dispersal may lower the frequency of sporophyte production, and thus the likelihood of becoming rare may increase in monoicous species (I).

Comparison of the production of asexual propagules with other reproductive characters, and with rarity, reveals differences in general patterns between British mosses (Longton 1992) and hepatics (paper I). A much higher proportion of hepatic species (46 %) produce asexual propagules, at least occasionally (I), than do the mosses (18 %, Longton 1992). In mosses, production of asexual propagules is closely related to dioicy (Longton 1992), which can be interpreted as a security system for hazardous sexual reproduction in species with separate sexes. In hepatics, however, production of asexual propagules does not seem to be related to sexuality, since the proportion of monoicous species that produce asexual propagules is nearly the same as that of dioicous species (I). Similarly, asexual propagation does not seem to be related to rarity in British hepatics: Again, about the same proportion of rare hepatic species produce asexual propagules as do the common species (I).

Interpretation of the results on the production of asexual propagules in the whole of the British hepatic flora leads to two conclusions: 1) Asexual reproduction functions as a security system for sexual reproduction liable to environmental disturbances such as drought and frost (see Longton 1990). 2) Asexual propagules function on a local level in maintaining populations, even though potential for dispersal may exist (Schuster 1988, see also Bolker & Pacala 1999). These conclusions are, however, far from exhaustive. The general pattern of asexuality among hepatics gives a background for empirical studies on individual species as model cases such as in the other papers presented here (II – V). The results in paper I give the motivation for testing the feasibility of the hypothesis derived from the aforementioned conclusions.

3.2. Ecological role of asexual reproduction in *Lophozia silvicola*

3.2.1. Colonization efficiency

The colonization efficiency of *Lophozia silvicola* is studied by two indirect methods (II), each of which represent a different successive stage of a colonization event (e.g. Hansson et al. 1992). The frequency of patches of occupied substrate provides an estimate of local dispersal ability, and the proportion of occupied substrate in the area available provides an estimate of the success of establishment. Söderström (1993) has suggested that the frequency of occupied patches corresponds to the likelihood of successful colonization in an area. Suitability of the substrate for colonization is, however, only rough and suggestive, although similar estimations have been used before (Söderström 1993).

In the study area in central Norway (II), local dispersal ability of *L. silvicola* seems fairly good, as on average 38 % of the available patches of substrate are occupied. Success of establishment, i.e. subsequent growth of the individuals and enlargement of the colony in size, is estimated by the proportion of the substrate area occupied. This is very small indeed, less than 0.1 %. As the number of asexual propagules produced in an area is relatively high (about 4000 gemmae per shoot, and more than 400 000 per colony area), the potential for local dispersal to new substrate patches seems good enough. Summarizing the circumstantial evidence on colonization efficiency, the critical stage seems to follow the arrival of propagules at a new patch, i.e. the establishment of a new colony following germination of propagules, and development and growth of new shoots (Söderström 1992).

The small colony size reflects recent colonization, and thus the young age of the colony (Söderström 1992, see also Piquot et al. 1998). Furthermore, the small average size of colonies of *L. silvicola*, in the study area in central Norway, can be interpreted as an indication of a relatively short turn-over time. As the frequency of sexual reproduction is very low, the number of gemmae produced seems to exceed the number of spores (see also Jonsson & Söderström 1988). This gives support to the hypothesis of asexual reproduction as the main means of maintaining the local population (e.g. Söderström & Herben 1997, see also Bolker & Pacala 1999). However, the actual dispersal range of propagules and the origin of colonies (i.e. whether germinated from spores dispersed from a distant population, or from locally produced gemmae) remains unknown.

3.2.2. Substrate preference and reproduction

Substrate optimality is derived from the observed occurrence and reproductive mode of colonies in a population of *Lophozia silvicola* in Kotinen Nature Reserve, southern Finland. The frequency of colonies on different substrates gives a preliminary indication of substrate preference (II, III), but of course, availability of the substrate types determines the actual frequencies on alternative substrates (see Culberson & Culberson 1982). In paper II, the estimation of the availability of potential substrates is largely based on experienced observations rather than exact measurements of substrate

quality. Microclimatic conditions may have an important role in determining the optimal site for a hepatic species. As shown by Clausen (1952), microclimatic conditions may vary considerably within a few centimeters of the substrate surface, as well as between patches in more exposed and more closed sites (Longton 1980). Additionally, competitive interactions between co-occurring species may alter the suitability of the substrate, even though niches of bryophytes often overlap (Söderström 1988a, Slack 1990, see also McAlister 1995). In paper III, only some substrate variables are measured (III), and interpretations are therefore tentative.

Lophozia silvicola colonies are found on three different substrate types (II, III, see chapter 2.6.). In the study area in southern Finland, 43.8 % of *L. silvicola* colonies are found on decaying wood, 44.6 % on soil, and 11.6 % on rock. Average colony size on the 50 x 50 m plot at Kotinen Nature Reserve was 99.6 cm² (III, see also paper V). Colony size does not seem to be related to the substrate type (III). A closer look at the substrate of decaying wood showed that *L. silvicola* has significant preferences for wood of a particular quality (see also McAlister 1995): *Picea abies* logs are more frequently occupied than predicted, as are also decorticated logs, and logs in advanced stage of decomposition. These results are in agreement with earlier observations made in northern Sweden by Söderström (1988b).

In *L. silvicola*, fertile colonies occur more frequently on decaying wood than on other types of substrate (III). Furthermore, fertile colonies are on average larger than NGB colonies. The fertility of a colony is likely to increase with its the age (see also Jonsson & Söderström 1988), as the likelihood of subsequent colonization events increases, and enhances the chances of both sexes to arriving at the same patch of substrate. It has been suggested, that sexual reproduction is an escape strategy from unfavourable conditions following, for example, the increased competition within a colony approaching the carrying capacity of the environment (see, however, Cockburn 1991). In leafy hepatics with facultative reproductive modes, I would, however, prefer to consider sexual reproduction as the principal strategy for population expansion, and asexual reproduction as a local maintenance strategy with dormant gemmae as a security potential in suboptimal habitats (see also paper I). Thus, on the basis of high incidence of sexual reproduction and large colony size on decaying wood, I consider this substrate type as optimal for *L. silvicola*. In contrast, a rock substrate seems to be only rarely occupied (see also paper II), and thus interpreted as suboptimal on the basis of small colony size and rare fertility, as suggested also by Söderström (1993).

3.2.3. Spatial distribution of colonies

The spatial distribution of the colonies was studied in a population of *Lophozia silvicola* in Kotinen Nature Reserve, southern Finland (III). The average distance between colonies in a 50x50 m plot was 1.94 m, a shorter distance than expected (2.36 m) on the basis of colony density and expected variance. In nearest-neighbour analysis (Campbell 1996) this mean distance gave an aggregated pattern of colonies (III), which was in agreement with my observations on the general pattern of substrate patches available in the study plot. The mean distance between colonies allowed an estimate of the dispersal range in an area, which illustrates the potential of the species for local dispersal. Obviously, the distribution of substrate patches determines the pattern, but is

also affected by the dispersal ability and competitive capacity of a species (Kimmerer 1994, Kimmerer & Young 1996). Further studies are still needed on the spatial population structure for *L. silvicola*, and for hepatics in general.

Distances between sexual and NGB colonies do not differ (III). This study fails to show a difference in dispersal ability between spores and asexual propagules in *L. silvicola*. Firstly, the observed spatial pattern reveals nothing about the origin of the colonies, whether germinated from locally or remotely produced diaspores, or how many separate colonisation events have occurred. Only in bisexual colonies is it obvious that at least two separate colonisations have occurred (Söderström 1992). Secondly, observed distances between colonies in an area do not reveal the actual dispersal ability of the species. As gemmiferous shoots in *L. silvicola* lack a specialized mechanism for the dispersal of gemmae, and most of the asexual propagules have been shown to fall close to their mother (see Crum 1972), dispersal distances of gemmae are unlikely to be very long (see, however, Schuster 1988). Experimental data on the dispersal range of gemmae in hepatics does not exist, and those available on mosses (Kimmerer 1994, Kimmerer & Young 1995) are in agreement with the aforementioned assumption.

3.3. Asexual reproductive effort in *Lophozia silvicola*

3.3.1. Biomass allocation

Dry weight is often used as an estimate of biomass that may be related to the production of sex organs and the vegetative growth of shoots, as biomass is easily converted to energy equivalents and represents the energetic component of the cost of reproduction (Rose & Bradley 1998, Valantin et al. 1999). Allocation of resources to alternative functions leads to a trade-off, which may occur also between facultative modes of reproduction (Karlsson & Pate 1992, Muir 1995, Seger & Eckhart 1996, Piquot et al. 1998, Nishitani et al. 1999). In bryophytes, such a trade-off has been reported in the mosses *Dicranum flagellare* and *Tetraphis pellucida* (Kimmerer 1994).

Allocation of biomass to reproductive organs is measured for the first time in leafy hepatics in paper IV. Allocation of total dry matter shows a possible trade-off between sexual and asexual reproduction in *Lophozia silvicola* (IV). Although gametangia-bearing shoots are able to produce asexual gemmae simultaneously with sex organs, a trade-off exists between the reproductive modes, with females bearing the highest costs for sexual reproduction. On average, NGB shoots produce three times more gemmae than female shoots, and male shoots twice as many (IV). In *L. silvicola*, the higher cost of reproduction to female plants is also indicated by the reduced length of shoots and in their differentiated branching pattern, as compared to males and NGB shoots (IV). Furthermore, females allocate on average 24 % of the biomass to the production of reproductive organs, while males allocate only 2.3 % (IV).

The results of this investigation into the allocation of biomass to facultative reproductive modes in *L. silvicola* are in agreement with the numerous studies on reproductive allocation in higher plants (see e.g. Karlsson & Pate 1992, Muir 1995). However, Degenkolbe (1938) states in his descriptive study on asexual propagation in

hepatics, that no antagonism occurs between the production of asexual propagules and sex organs. Indeed, in hepatics the production of chlorophyllose sex organs may be facilitated by the ancillary reproductive structures themselves. For instance, in algae with sex organs capable of photosynthesis, reproduction is likely to be cost-free (DeWreede & Klinger 1988). The cost of reproduction is higher for females than for males, which is the common, if not the exclusive case, among higher plants (Cox 1988) and other organisms (Rose & Bradley 1998). In addition to sex, allocation of resources to reproduction is dependent on environmental conditions (see Busso et al. 1998) and on the size of plants (Sugiyama & Bazzaz 1998). Life history evolution including sexuality traits, functions principally on fitness components, expressed in numbers of off-spring produced, and on mortality. Presently, few data on mortality in colonies of *L. silvicola* are available (paper V), but my preliminary observations at Kotinen Nature Reserve indicate high mortality among females subsequent to sporophyte production (see also Duckett & Renzaglia 1993).

The higher cost of sexual reproduction, as compared to asexual reproduction and vegetative growth, has consequences on species ecology. Asexual reproduction by mitotic gemmae is less costly than sexual reproduction in *Lophozia silvicola* (IV). Similarly, the production of vegetative propagules in higher plants as has been shown to be less costly than sexual reproduction (e.g. Nishitani et al. 1999). Callaghan et al. (1997) and Jónsdóttir & Watson (1997) demonstrated that clonal spread by vegetative or asexual propagules is an adaptive strategy in severe conditions, and in temporal habitats with a high chance of stochastic disturbances (see During 1992). Differential success in establishment of spores and asexual propagules has been shown in Kimmerer's (1991b) study on the moss *Tetraphis pellucida*. The superior ability of asexual propagules to germinate and become established secures colonization and the maintenance of the population at less cost than would be allowed by the production of sexual progeny. Furthermore, Newton & Mishler (1994) have discussed different ecological roles of spores and asexual propagules in the dispersal and dynamics of bryophyte populations. Production of spores, as a costly result of sexual reproduction, is profitable only when an excess of resources for reproduction are available (see III), and dispersal to new patches of habitat is likely to considerably affect the survival of the population (see also Söderström & Herben 1997, Husband & Barrett 1996).

3.3.2. Presence and periodicity of gemmae

The presence of gemmae on shoots of *Lophozia silvicola* is easily measured by the method applied in papers II, IV and V (chapter 2.4, see also Söderström 1994). Unfortunately, it does not give a direct estimate for the production of gemmae, which requires further experimental work in laboratory conditions. In the two study areas, the average number of gemmae present on shoots varied from 1000 to almost 7000 (II, V). Given the density of shoots, the number of gemmae present can easily be extrapolated to the number of propagules present per colony area (from 4×10^5 to more than 6×10^6 , paper II). The number of gemmae present in colonies of *L. silvicola* are highly competitive with the 86 000 spores per capsule reported by Jonsson & Söderström (1988). This method is also applicable to other gemmiferous leafy hepatics.

Periodicity in production of asexual propagules is dependent on the species and on the environment. Though rarely demonstrated in bryophytes, some indication of periodicity in asexual propagation is available on mosses (Odu & Owotomo 1982, Reese 1984) and on hepatics (Degenkolbe 1938). However, Schuster (1988) and Duckett & Renzaglia (1993) report asexual propagules present on shoots or thalli of hepatics throughout the growing season. In tropical hepatics lack of periodicity seems obvious (see Schuster 1988). Although gemmae are present on thalli of *Blasia pusilla* throughout the growing season, gemmae produced at the beginning of the season are of a different form to those produced at the end (Duckett & Renzaglia 1993). This indicates some form of seasonal regulation of gemma production. My results on *Lophozia silvicola* show a slightly parabolic trend (V) in average numbers of gemmae present on shoots during the growing season, even though no significant differences in numbers are found (II, V). However, on the basis of Buch's (1911) and Degenkolbe's (1938) descriptions on the development of gemmae in a seasonal climate, a certain periodicity in gemma production is a biologically relevant assumption (see paper V).

As gemmae are produced by mitotic cell divisions in specialized cells on leaf lamina tissue, their production and development might well be susceptible to similar environmental regulation of growth as gametophytic tissues in general (see e.g. Longton 1980, Sveinbjörnsson & Oechel 1992). Growth conditions vary between localities and between years, possibly explaining high variability between colonies of *Lophozia silvicola*, and between sampling periods (II, V, see also Shaw 1990). Additionally, allocation of resources between sexual and asexual reproduction is likely to decrease the numbers of gemmae present in bisexual colonies, as the higher cost of producing sex organs lowers the numbers of gemmae produced in female and male individuals (IV).

3.3.3. *Effect of colony density*

In bryophytes, more or less contradictory results have been reported on the effect of colony density on growth and survival of individual shoots and on reproductive success. In some species, growth is enhanced with increasing density (e.g. During 1990), as might be expected in ectohydric plants (see also Økland & Økland 1996). In other cases, negative effects of increasing density on growth and branching are demonstrated (Clymo 1970, Bates 1988). In some species, shoot mortality declines with increasing density (e.g. Watson 1979), but in some cases the opposite is shown (Kimmerer 1991a). However, all the studies on density-dependence in bryophytes have been done on mosses, and no such data are available on hepatics, except the results presented in paper II.

Sexual reproduction is very likely to be affected by the colony density, as fertilization is dependent on the capacity of motile sperms to reach the archegonia. For hepatics that lack specialized devices for sperm dispersal (such as splash-cups found in some mosses, see e.g. Longton & Schuster 1983), the distance between male and female organs becomes crucial for reproductive success. The range of distances for sperm dispersal are generally shown to be very short, only a few centimeters (Wyatt 1982, Longton & Schuster 1983). In dioicous species, the problem becomes even more pronounced. However, very few data are available on the effects of shoot density

within a colony. Kimmerer (1991a) has shown in her study on the moss *Tetraphis pellucida*, that the prevailing mode of reproduction is related to shoot density. At low densities asexual reproduction is predominant, while at high densities sexual reproduction is prevalent (Kimmerer 1991a).

The shoot density in colonies of *Lophozia silvicola* appears to be fairly constant between the sampling periods, and between the colonies (II, V). On average, colony density in Kotinen Nature Reserve is 21 individual shoots per 1 cm² sample (V). In the study locality in central Norway, the densities are a little higher, 22-29 shoots per cm². The shoot densities were measured in the colonies used for repeated sampling (II, V), but as the colony density does not vary significantly during the season, no effect of sampling on the colony dynamics is assumed. It must be noted, that the variability in the size of the individual shoots increases during the growing season (under prep.), but the number of shoots does not change (II, V). In the study area in central Norway no correlation was detected between the average number of gemmae present on shoots and the density of colonies (II). I have made similar observations in the study area in the Kotinen Forest Reserve (under prep.). The lack of density-dependence in asexual reproduction may, again, give support to the maintaining role of asexual reproduction in a patchy habitat with possibly low long-distance dispersal (paper I, see also Pettersson 1997, Bolker & Pacala 1999).

3.4. Evolution of dormancy in gemmae of *Lophozia silvicola*

In the evolution of life histories, selection may influence the timing of reproduction. Dormancy of propagules is widespread in organisms inhabiting unpredictably varying environments (e.g. Evans & Cabin 1995). Dormancy has been considered as a risk-spreading strategy, which enhances survival and the effective use of resources. It lowers the negative effects of competition, especially in heterogeneous environments (e.g. Rees 1996, Hyatt & Evans 1998). Furthermore, dormancy has been seen as an alternative strategy to dispersal (e.g. Cohen & Levin 1991, McPeck & Kalisz 1998). On the basis of McPeck & Kalisz's (1998) view of dormancy and dispersal as facultative strategies in patchy habitats with randomly varying within-patch fitnesses, an analogy can be drawn to facultative roles of reproductive modes (see Newton & Mishler 1994). Both strategies are maintained with some frequency to ensure the species survival.

The timing of production and development of new individuals have a specific importance in a periodically changing environment. In hepatics, nearly nothing is known about the germination of spores or asexual propagules in nature (Longton & Schuster 1983). Although dormancy has been reported in moss spores (During 1979), it seems not to be the rule (Longton & Schuster 1983). However, Duckett and Renzaglia (1993) report dormancy in gemmae of *Blasia pusilla*, and indirect evidence of dormant hepatic propagules, including *Lophozia* spp., is available on study of a diaspore bank (Jonsson 1993, Bisang 1996).

The original observation of decreasing germinability in liquid culture of *Lophozia silvicola* gemmae towards the end of the growing season (paper II) motivated consideration of the destiny of the non-germinating gemmae. The results of research by

Duckett & Renzaglia (1993) on the different roles of morphologically distinct forms of readily germinating and over-wintering gemmae in the thalloid hepatic *Blasia pusilla*, gave us an idea of increasing the proportion of gemmae entering dormancy at the end of the season (V). In the first place, a theoretical approach to evolutionary profitability of dormancy in asexual propagules of *Lophozia silvicola* is simulated in the paper V, by a model constructed on the basis of real population parameters obtained from a population at Kotinen Nature Reserve. The aim is to test, whether such a life history strategy is realistic in this species. If so, the next step will be an experimental approach to confirm the existence of dormancy, and its population dynamic role.

The germinability of gemmae in *L. silvicola* clearly decreases in liquid culture during the growing season (II, V). In each of the three years of this study, the average germinability decreased from 60 % to about 20 % from the first sampling in May to the last in October. Though variation in germinability is observed between localities (II, V) and between years (V), the general trend is similar. The proportion of dead shoots in the colonies of *L. silvicola* were used as a rough estimate of shoot mortality. The average mortality appears to be about 3 % during the growing season, and about 10 % in winter (V). However, as extrapolated over the whole of the growing season, most of the mortality in the colonies of *L. silvicola* occurred during the summer. Mortality of gemmae was relatively high in the culture. About 50 % of the non-germinated gemmae died. As no direct measurements on survival of each proposed gemma type, dormant and non-dormant, were available, the proportion of both types were estimated as equal in the model parameterisation (see Chapter 2.8.).

The simulation results support our hypothesis of gemmae entering dormancy in *Lophozia silvicola* (V). Relative values of dormant and non-dormant gemmae influenced the quantitative predictions in a realistic way. For instance, an increase in the winter mortality of shoots favours an increase in the fraction of dormant gemmae produced, especially towards the end of the growing season (V). The simulated germinability schedule follows a similar pattern to the observed schedule, although the predicted germinability is somewhat higher than that observed in a natural population. In colonies of *L. silvicola*, non-dormant gemmae germinate during the growing season whenever space becomes available. Early in the season, empty patches of substrate, created by disturbances and mortality during winter, are quickly colonized by over-wintered dormant gemmae (see also Bolker & Pacala 1999). The local dynamics described here appear realistic, but no data is yet available on demographic processes in colonies of *L. silvicola*. Dormancy of gemmae seems an appropriate explanation for observed decreasing germinability (II, V). However, experimental verification is still needed.

4 CONCLUSIONS

The results of this thesis raise further questions rather than arrive at the final truth. However, some preliminary answers are given to the basic questions addressed in chapter 1.3.: 1) Asexual propagation is common among hepatics. It is, however, not directly correlated either to sexuality as in mosses (Longton 1992), or to rarity. The results support the role of asexual propagation in local dynamics. 2) An easy quantitative method for estimation of asexual propagation in gemmiferous hepatics is

described in paper II (see also Chapter 2.4.), and further applied in papers IV and V. The results obtained by this method can be extrapolated from individual shoots to population level. The method does not, however, give direct measure of gemma production. 3) An indication of a trade-off between sexual and asexual reproduction in *Lophozia silvicola* is presented in paper IV. Allocation of biomass to sexual reproduction seems to reduce the length of the shoots, and to regulate the branching pattern. Furthermore, in the dioicous *L. silvicola*, allocation of biomass to sexual reproductive organs is shown to be much higher in females than in males. 4) In *L. silvicola*, the frequency of fertile colonies is higher on decaying wood as compared to other substrate types. Substrate optimality is presented as a possible explanation for larger colony size and more frequent sexual reproduction on logs (III). Clear preference of *L. silvicola* for the quality of decaying wood as a substrate are shown. No connections between reproductive modes and spatial pattern of the population are shown here. The proportion of occupied potentially available patches of substrate is used as an estimate of colonisation efficiency (II). The proportion of the potential substrate surface occupied is used as an estimate of success of establishment (II). No direct measure of colonisation efficiency is used. 5) The hypothesis that there is an increasing proportion of gemmae entering dormancy towards the end of the growing season is tested by an individual-based cellular-automata model. The simulations based on the model parameters, estimated from real data on *L. silvicola*, give support to the hypothesis of gemma dormancy. Thus, gemma dormancy can be seen as a realistically adaptive strategy, the existence of which, however, still requires experimental verification.

The results presented here challenge some general theories on evolution of life histories and on the role of asexual reproduction. It has generally been argued that sex is costly (e.g. Crow 1994). With high cost of sex, some extra advantages are gained. In asexual reproduction, these advantages are lost, even though some substitution is provided by an energetically less costly mode of reproduction. Most of the terrestrial multicellular organisms reproduce sexually, asexual species being short-lived offshoots of sexual lineages, even evolutionary dead-ends (e.g. Smith 1978, Crow 1994). However, in hepatics as a relatively large and ancient (see Edwards et al. 1998) group of plants, asexual reproduction is common (I) and seemingly an adaptive strategy (Mishler 1988, see also Newton & Mishler 1994). Even the genetic variability in hepatic populations has prevailed to be higher than expected, though lower than in mosses (Wyatt 1994). When considering hepatic species with frequent asexual reproduction, one should put conventional ideas aside and take a closer look at facultative modes of reproduction and the evolutionary potential of the species.

The results of my research give circumstantial support to the hypothesis that asexual reproduction functions on a local level in the maintenance and dynamics of populations. As suggested by Söderström & Herben (1997), without external disturbances bryophyte populations with effective asexual propagation may persist indefinitely. In a temporally and spatially heterogenous habitat, however, mere "sitting" on a patch once occupied does not adequately ensure the survival of a population. Almost exclusive production of gemmae in colonies of *Lophozia silvicola* emphasize the significance of asexual reproduction as an adaptive and even primary reproductive strategy in this species. Delayed development of a proportion of gemmae produced may well be an indication of a highly specialized adaptive life history strategy in *L.*

silvicola. The prevalence of asexuality is, however, obscured by occasional sexual reproduction. The energetic cost of the production of sex organs is considerable, and reflected also in the numbers of gemmae produced, indicating a trade-off between the two reproductive modes. Maintenance of local colonies facilitated by dormant gemmae is completed by the facultative strategy of dispersal by spores produced as a result of sexual reproduction. The importance of local dynamics puts forward a special demand for conservation acts to protect natural habitats of species with a similar ecology and reproductive system to those of *L. silvicola* (see Dettki et al. 1998).

Although no direct evidence is yet available on the genetic consequences of sexual and asexual reproduction in *Lophozia silvicola*, occasional sexual reproduction may function as a generator for enhanced genetic variability, and thus for higher evolutionary potential. On the other hand, an almost unexplored field is the genetic variability caused by somatic mutations (see Mishler 1988, Newton 1990) transmitted by asexual propagation, and directly expressed in haploid gametophytic individuals (Wyatt 1994). If the last-mentioned possibility is true in hepatics, theories on the evolution of sex are seriously challenged (see also Klekowski 1997). One should keep in mind that what is true in one organism, may not be so in another. Searching for "rules in nature" (see Hanski 1982) may just be an expression of individual ambition.

The last concluding observation of this thesis is that very little indeed is known about reproductive ecology and the population dynamics of hepatics. With such small samples, such simple questions and such modest methods as those used here, it is embarrassing to stand as a pioneer in this special field of population ecology. I can only wish, that somebody takes up the challenge and continues looking for answers to some of those many questions that have been raised by this study.

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