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Establishment, Growth and Population Dynamics in two Mosses of Old-growth Forests

BY

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Abstract

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Biodiversity in forests depends on long canopy continuity and existence of different elements which function as substrates for varying organisms. Bryophytes often occupy specific substrates with a patchy distribution. The aim of this thesis was to increase the ecological knowledge about two threatened moss species; *Buxbaumia viridis*, inhabiting decaying wood, and *Neckera pennata*, inhabiting bark of base-rich deciduous trees.

Establishment from spores was investigated in *Buxbaumia viridis* and *Neckera pennata* and models were created to predict germination of spores as a function of pH and water potential. The effects of pH, phosphorus and nitrogen concentration were studied in *Buxbaumia viridis*, both on spore germination and on sporophyte occurrences in the field. Colony growth in relation to precipitation and microhabitat variables was studied in *Neckera pennata*, and a model was used to predict growth of colonies over time. Metapopulation dynamics of *Buxbaumia viridis* were analyzed as an effect of precipitation, habitat quality and patch quantity. A spatial explicit patch occupancy model was constructed to simulate metapopulation sizes and extinction risk over 100 years.

The quality of the substrate was very important for spore establishment. Germination success increased with increasing pH in both species. *Buxbaumia viridis* was less sensitive to low pH than *Neckera pennata* when water was freely available. However, there was a strong interaction between pH and water potential in prediction of the final cumulative germination: the spores reacted positively to one factor only when the other factor was in a favourable range.

Precipitation, moisture holding capacity and interference competition were the main factors affecting colony growth of *Neckera pennata*. *Buxbaumia viridis* showed large fluctuations in number of occupied patches among years. Both colonizations and extinctions were highly related to precipitation. Spore germination and sporophyte occurrences in the field were positively related to phosphorus concentration and pH of the substrate.

Keywords: Buxbaumia viridis, *Neckera pennata*, bryophyte, pH, phosphorus, water potential, precipitation, metapopulation, environmental stochasticity, ecology, plant

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Till min älskade familj:
Lasse, Henrik och Arvid

List of Papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals.

I. Wiklund K. 2002. Substratum preference, spore output and temporal variation in sporophyte production of the epixylic moss *Buxbaumia viridis*. Journal of Bryology 24: 187-195.

II. Wiklund K. 2003. Phosphorus concentration and pH in decaying wood affect establishment of the red-listed moss *Buxbaumia viridis*. Canadian Journal of Botany 81: 541-549.

III. Wiklund K and Rydin H. Ecological constraints on spore establishment. Functional Ecology: in press.

IV. Wiklund K. och Rydin H. 2004. Colony expansion of *Neckera pennata*: modelled growth rate and effect of microhabitat, competition and precipitation. The Bryologist 107: in press.

V. Wiklund K. Metapopulation dynamics of a short-lived moss, driven by precipitation and habitat quantity. Manuscript.

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Contents

Introduction

Forests are indispensable in many aspects and there is an inevitable conflict between timber or pulp-wood production and biodiversity. In Sweden, both should be considered equally important (Anonymous 1992) and we have a parliamentary resolution for “sustainable forests” that should be fulfilled by 2020 (SOU 2000).

Biodiversity in forests depends on long canopy continuity and existence of different elements which function as substrates for varying organisms. Most important are old trees, decaying wood and deciduous trees (Berg et al. 1994; Esseen et al. 1997; Ohlson et al. 1997; Berg et al. 2002), and many species, but not all, dependent of these substrates are considered to be threatened (Gärdenfors 2000). Why are some species more infrequent than others, and, do rare species have special characteristics separating them from common species? To answer such questions, and to facilitate a forest management taking both biomass production and biodiversity into consideration, it is important to increase our knowledge about threatened species. With this thesis I try to add a small piece to that large puzzle.

Bryophytes in old-growth forests

Bryophytes contribute significantly to boreal and temperate forest biodiversity. Some species are drought resistant and struggle on boulders and tree stems where vascular plants are excluded. Other species make use of the higher moisture in decaying logs and stumps, forming a beautiful and often diverse carpet on wood surfaces. In the boreal forests, bryophytes flourish in the forest floor.

Species richness of bryophytes are higher in old-growth forests than in managed stands (Söderström 1988a; Andersson & Hytteborn 1991; Lesica et al. 1991) and bryophytes, together with lichens and other fungi, are commonly used as indicators of valuable forests in Sweden (Nitare 2000).

Why are some species rare?

Although with many exceptions, rare species seem to differ from common ones in a number of ways (Gaston & Kunin 1997; Rosenzweig & Lomolino 1997; Longton & Hedderson 2000). In this thesis I discuss rarity in connection with habitat specificity and population dynamics.

Requirement of very specific habitats are thought to be one main characteristic predisposing rarity and species with such requirements should have a narrow fundamental niche breadth. Further, they often seem to require scarce habitats, which in addition often are productive (Rosenzweig & Lomolino 1997). Habitat specificity and niche breadth among plants could be manifested in the fundamental niche of adults or in the regeneration niche (Grubb 1977) during establishment. Species can also be rare in time (Harper 1981), and to reveal patterns of population dynamics, long-term studies are needed.

There are many ways in which a species can be rare (Rabinowitz 1981) and it seems logical to think that formerly common species, which have become rare, have a higher risk of extinction than species with a long continuity of rarity (Kunin & Gaston 1993; Mace & Kershaw 1997). Modern forestry practices with fragmentation of old-growth stands, drainage by ditches, reduced quantity of coarse woody debris and fewer deciduous trees have resulted in declining populations of many species, and among them many bryophytes (Esseen et al. 1997; Gärdenfors 2000). Air pollution is an additional cause of declining populations of some epiphytic bryophytes (Hallingbäck 1992; Sjögren 1995).

Establishment – windows of opportunity

Bryophytes lack roots and basically they get water and nutrients from precipitation. As a result, substrate quality might have the highest influence on bryophytes during the establishment stage (Brown 1982; Bates & Bakken 1998). Bryophytes can establish new plants from spores, specialized asexual propagules or from fragments. Asexual diaspores generally seem to have higher establishment success than spores (Keever 1957; Miles & Longton 1990; Kimmerer 1991), but the spores are smaller and have potential for long-distance dispersal (van Zanten & Pócs 1981; Muñoz et al. 2004).

Spores germinate readily in controlled experiments. Water is vital for spore germination, but also pH (Cameron & Wyatt 1989; Thomas et al. 1994), phosphorus (Boatman & Lark 1971; Sundberg & Rydin 2002), temperature (Newton 1972) and light (Forman 1964) affect germination. The importance of establishment from spores in the field is to a large extent unknown, but seems to vary among life-history strategies. In a field experiment the fugitive species was the only one developing protonemata and shoots from spores, while the long-lived perennial and the colonists did not show any conclusive evidence of germination (Miles & Longton 1990). However, it is possible, and even probable, that establishment from spores occurs in almost all species, but that germination in nature occurs infrequently during short temporary windows of opportunity, when conditions for germination are favourable. Those rare events, probably governed by precipitation, might be extremely important for the foundation of new colonies.

The knowledge about establishment requirements in bryophytes is very restricted (Bates 2000) and investigations of rare species are sparse, though it is possible that establishment events are limiting for their distributions. Hence, increased understanding of establishment probability during different environmental conditions is central for conservation and management of bryophyte species.

Growth

Compared with vascular plants bryophytes generally have low relative growth rate and, except for the short-lived ruderals, all bryophytes have been classified as stress tolerators (Grime et al. 1990). However, there is a large variation in potential relative growth rate among different bryophyte species (Furness & Grime 1982).

In many bryophyte habitats, water is the most limiting factor for growth. Photosynthetic assimilation is possible only if the moss is wet (Tallis 1959; Proctor 1972; Busby et al. 1978) and several studies have demonstrated a clear positive relationship between precipitation and growth (Tallis 1959; Pitkin 1975; Busby et al. 1978; Backéus 1988; Vitt 1990). In some studies, growth of the investigated species was not not correlated with precipitation but instead with air temperature (Bates 1989; Zechmeister 1995). However, most boreal bryophytes are adapted to grow at low temperature. They have lower temperature optimum than temperate vascular plants (Tallis 1964; Furness & Grime 1982) and show substantial growth already at 5 °C (Pitkin 1975; Furness & Grime 1982). Besides the climatic factors, light (Tamm 1953; Miyata & Hosokawa 1961; Rincon & Grime 1989), nutrient supply (Tamm 1953; Skre & Oechel 1979) and pH of the substrate (Pitkin 1975) have been shown to affect growth. Growth in bryophytes often shows a positive density-dependence (Bates 1988; Økland & Økland 1996) and it is possible that competition among bryophytes is mainly for space and not for resources (Økland 1994).

Modern forestry practices alter the microhabitat, which can have severe effect on some bryophytes even when the substrate itself remains. In sensitive species, shoots exposed to long dry periods (Proctor 1972) or repeated desiccation (Schipperges & Rydin 1998) might die.

Metapopulation dynamics

Bryophytes frequently inhabit patchy and clearly delimited substrates, such as tree stems, boulders and decaying wood. Both living and dead trees are temporary habitats with final deterministic disappearance. Species dependent on such substrates are likely to form metapopulations (Hanski & Hammond 1995). A typical feature of metapopulations is that they do not occupy all suitable patches. In classical metapopulation theory all patches are equal and an equilibrium fraction of occupied patches exists, predicting that metapopulations will persist as long as colonization rate is higher than extinction rate (Hanski 1998). The classical model (Levins 1969) predicts that the fraction of occupied patches at equilibrium increases with increasing patch size and with increasing patch density. These forecasts have generally been supported by empirical studies (Verboom et al. 1991; Hanski 1994; Hanski et al. 1995; Ericson et al. 1999). In reality all patches are not equally suitable, and including habitat quality in metapopulation models have usually improved model fit (Verboom et al. 1991; Moilanen & Hanski 1998; Fred & Brommer 2003; Johansson & Ehrlén 2003). Incorporating spatial structure have increased reality in the models (e.g. Lamberson et al. 1992; Hanski & Thomas 1994; Snäll et al. 2003). However, metapopulation models have mostly disregarded correlated environmental stochasticity, e.g. weather factors, which affects all patches synchronously and might increase global extinction risk (Harrison & Quinn 1989; Wichmann et al. 2003).

Reduction in quantity of coarse woody debris by altered forest management is one of the most obvious and important changes in boreal forests in the 20th century (Kirby et al. 1991; Östlund et al. 1997). Using a metapopulation approach to study the population dynamics on dead wood patches, will increase knowledge about how to conserve such species (Hanski & Hammond 1995).

Aims

The aim of this thesis was to increase the ecological knowledge about two threatened moss species, inhabiting two of the most important substrates for bryophyte diversity in the boreal forests: decaying wood and base-rich deciduous trees.

The following topics are treated in the thesis:

- how pH and availability of nitrogen, phosphorus and water affect spore germination and early protonemal growth in *Buxbaumia viridis* and *Neckera pennata* (**II**, **III**)
- how precipitation affects growth of *Neckera pennata* (**IV**) and population dynamics of *Buxbaumia viridis* (**V**)
- how different habitat factors affect occupancy, colonizations and extinctions in metapopulations of *Buxbaumia viridis* (**I**,**V**) and how different habitat quantity affects metapopulation extinction risk (**V**)
- how different habitat factors affect colony growth of *Neckera pennata* and the time needed to attain a certain colony size as well as age of first reproduction (**IV**)
- life cycle, spore output (**I**) and metapopulation dynamics (**V**) in *Buxbaumia viridis*

Study species

Buxbaumia viridis

Buxbaumia viridis (DC) Moug. & Nestl. is a dioicous short-lived moss growing on decaying wood and humus in coniferous and deciduous forests (Smith 1978; Nyholm 1979b). The gametophyte is minute, consisting only of a filamentous protonema and bracts with reproductive organs formed at the apices of the protonemal branches (Nishida 1978). The sporophyte is relatively large; a full grown sporophyte varies in length from 7 to 25 mm (Möller 1923). Each spore capsule contains a high number of spores: 1.4 to 9.0 millions with a mean value of 6.0 millions, where spore number is correlated to capsule size (**I**). According to Boros & Járai-Komlódi (1975) the spores have a mean diameter of 11.9 µm with a range of 8.8-14.7 µm. The peristome of *B. viridis* has no active function in spore dispersal, instead the spores are ejected by raindrops compressing an air space within the capsule (Schofield 1985).

Since the gametophyte is hard to detect in the field, the life cycle of *B. viridis* is not very well known. Möller (1923) reports findings of antheridia and archegonia in *Buxbaumia aphylla* from end of May to middle of June. He had, however, never found sex organs in *B. viridis.* In one of my study areas I have seen inflorescences, predominantly males, of *B. viridis* in April-June and very early stages of a few sporophytes in late May. The female plants seemed to develop at deeper positions of the wood than the males. Little is known about life span of the protonemata, but they might possibly persist for several years, as has been suggested for *B. aphylla* (Hancock & Brassard 1974). In eastern central Sweden, sporophytes are normally found in October (late September in wet autumns and not until November in very dry autumns) and most spores are released in middle of June the following year. The mature sporophytes often remain when the next year's sporophytes are formed; hence it is possible to find sporophytes all the year round.

Based on findings of sex organs as early as April, i.e. prior to spore release, and on logistic regression of colonizations which indicated that the new sporophytes were derived from sporophytes formed two years earlier (**V**), I suggest the following life cycle for *B. viridis*: Mature spores are released in June year one and the spores germinate and form protonema during favourable periods. Antheridia and archegonia are formed in spring (April-June), and fertilization occurs in May-June, year two. Early stages of sporophytes develop during the summer and the setae are elongated in September-October year two. The mature spores are released in June year three. If the protonema survives, it can possibly form new gametangia in spring year three. Populations can also persist with brood cells, i.e. swollen globular drought tolerant cells (Goode et al. 1993), broken from the protonemata. This phenomenon I have observed in old agar cultures.

It has been suggested that *B. viridis* is saprophytic (Haberlandt 1886 in Dening 1928) and several sources (Smith 1978; ECCB 1995) state that the protonema is brown. Both cultivated and wild protonemata are green and photosynthetic, but the male and female bracts turn into brown. Thus, there is no reason to suspect a saprophytic life style, which was also concluded by Dening already in 1928 and later by Duckett et al. (2004).

B. viridis has a widespread circumboreal distribution, but appears to be rather uncommon anywhere it occurs. In Sweden it is classified as near threatened (Gärdenfors 2000) and in Europe as vulnerable (ECCB 1995). It is also include in Annex 2 of the EU Habitat Directive. In the United States it is listed among sensitive and rare mosses closely associated with old-growth forests (Thomas et al. 1993; Christy & Wagner 1996). The species occurs also in China (Smith 1978).

Neckera pennata

Neckera pennata Hedw. is a large autoicous moss growing mainly on trunks of deciduous trees (Nyholm 1979a). It is a perennial long-lived species which spread over the bark by stoloniferous primary stems on which secondary decumbent shoots are formed. Capsules are located on short setae on the lower side of the secondary shoots. In my study areas, investigated colonies formed capsule for the first time at a colony size of 12-79 cm^2, corresponding to an estimated age of 19-29 years (**IV**), and capsules are common on colonies larger than 100 cm^2 (Hagström 1998). A capsule contains about 90.000 spores (Hagström 1998) with a size of 24µm (Nyholm 1979a). In eastern central Sweden, the spores are dispersed from late autumn to very early spring. Based on behaviour of the peristome teeth (Patterson 1953), which form an open grid when dry, I conclude that spores of *N. pennata* are dispersed during dry weather conditions.

The metapopulation dynamics of *N. pennata* has been characterized as patch-tracking, colonization occurred mainly in the vicinity of occupied trees, and local extinction was caused mostly by tree fall (Snäll 2003; Snäll et al. 2004).

N. pennata has a wide distribution with occurrences in Europe, North and South America, Asia, Africa and Australia (ECCB 1995). The species is classified as vulnerable in Sweden (Gärdenfors 2000) as well as in Europe (ECCB 1995), and seems to indicate old-growth forests (Frahm 1992; Kuusinen & Penttinen 1999; McGee & Kimmerer 2002).

Methods

Study sites and climate

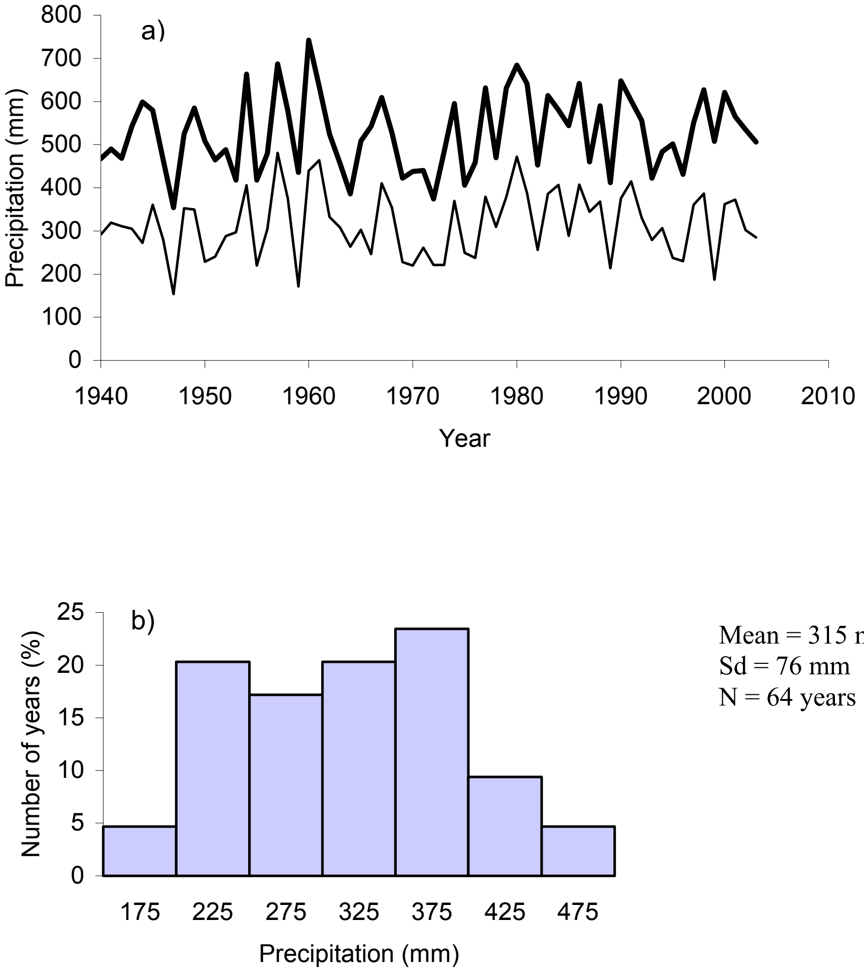
The study sites are located within the boreo-nemoral (hemi-boreal) vegetation zone (Sjörs 1999), in the province of Uppland, eastern central Sweden. This is an agricultural region at low altitude, which was covered with water when the ice border retreated after last glaciation. The investigated sites are situated at 15-30 m above sea level and the quaternary deposits consist of glacial clay or sandy till.

The field studies of *B. viridis* (**I, II, V**) were performed in two forests close to Uppsala. In these, *Picea abies*, *Populus tremula* and *Betula pendula* were the most abundant tree species, but also other deciduous trees occurred. The field study of *N. pennata* (**IV**) was carried out in the vicinity of Lake Vällen, in eastern Uppland. Three forest sites with high abundance of broad-leaved trees, such as *Fraxinus excelsior*, *Acer platanoides*, *Ulmus glabra*, *Tilia cordata*, *Quercus robur* and *Populus tremula*, were used. The field-layers in all investigated forest sites were herb-rich.

The length of the climatic growing season (threshold +5°C) is *ca* 190 days (Sjörs 1999) and the mean annual precipitation, as measured in Uppsala 1961-1990, was 544 mm (Alexandersson & Eggertsson Karlström 2001). Precipitation data were obtained from the Erken Laboratory, Uppsala University (**III**) and from Ultuna Climate Station, Swedish University of Agricultural Sciences (**I, V**). Precipitation in 1940-2003 at one of the investigated sites is shown in Fig. 1.

Establishment experiments

Germination of spores is difficult to study in the field because the spores and protonemata are hard to detect on natural substrates. Use of bark or wood in laboratory experiments pose a problem since natural substrates are inhabited by fungi or algae, and sterilization alters the substrate chemistry . Culture media offers a practical alternative. A challenge of *in vitro* cultivations is to mimic the range of moisture conditions normally occurring in the field. Water potential is widely used for quantifying the energy state of water



Mean = 315 mm
Sd = 76 mm
N = 64 years

Fig. 1. Precipitation at Vipängen (forest II in paper I and V) between 1940 and 2003. a) Precipitation as sum over each year (upper curve) and between May and October (lower curve). b) Frequency of years (%) with different May-October precipitation. Figures on the abscissa represent class midpoints. Data from Ultuna Climate Station, Swedish University of Agricultural Sciences.

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in soil and organic materials (Papendick & Campbell 1981) and polyethylene glycol (PEG) has commonly been used to maintain cultivation media at fixed water potentials. PEG is a long-chain inert organic polymer that alters the matric potential of the solution (Steuter et al. 1981).

In my experiments I have used solidified (Bacto agar Difco) (**II**) and liquid (**III**) culture media. Spore germination is easy to observe in liquid media, but for a more normal protonema and shoot growth, solidified media is recommended (Duckett et al. 2004). In different experiments (**II, III**) I manipulated pH, total nutrient concentration, nitrogen, phosphorus and water potential (using PEG 6000) in the media. The same relationship between different nutrients was used in all experiments, and it was based on ratios shown to be required for unimpaired growth in different vascular plants (Ericsson 1994).

Cultures were started with spores from *B. viridis* (**II, III**) and *N. pennata* (**III**). The moss capsules were surface sterilized 1.5 minute in 1.5% (v/v) sodium hypochlorite solution. The sodium hypochlorite had a very high pH, and since pH was included as a treatment, careful washing in distilled water was necessary before the spores were added to the culture media. Only capsules with a green vital spore mass were used.

The spores sink to the bottom in liquid media, and if too much spores were added, germination was prevented. Still, the concentration needed to be high enough to make counting of germinated spores practical. I used a concentration of 305 and 145 spores per 9 cm Petri dishes with agar, and approximately 4000-6000 spores ml^{-1} in Erlenmeyer flasks containing 10 ml nutrient solution. The cultures were incubated in growth chambers and the proportion of germinated spores, and protonemal sizes, were assessed under a stereo microscope (**II**) or a light microscope (**III**).

To compare the results from the experiments with the quality of dead wood in the field, wood samples with and without sporophytes of *B. viridis* were analyzed for pH, phosphorus and nitrogen (**II**).

Growth studies

Absolute growth rate was used when calculating protonemal growth of the *in vitro* experiments (**II, III**), while relative growth rate was used in calculations of colony growth of *N. pennata* in the field (**IV**). Absolute protonemal growth rate was calculated as:

$$\text{Growth} = (N_{t1} - N_{t0}) \times (t1 - t0)^{-1} \qquad \text{equ(1)}$$

where N_t is number of cells at time t. Relative growth rate (RGR) was calculated as:

$$\mathrm{RGR} = (\ln A_{t1} - \ln A_{t0}) / \Delta t \qquad \text{equ(2)}$$

where A_t is colony area at time t1 and A_0 is colony area at time t0.

Colony sizes and number of fertile secondary shoots were measured on small colonies (< 100 cm^2) of *N. pennata.* The peripheries of the colonies were drawn on plastic sheets on five occasions between August 2000 and July 2003. The following habitat variables were measured: host tree species, any tree species with its crown projecting above the investigated colony, stem diameter at 1.3 m, depths of bark fissures, direction of exposure, stem slope, height on stem, height from ground, bark pH, bark moisture, soil moisture, cover of other epiphytes in classes of 10% within 1.5 cm around periphery of the *N. pennata* colony. Bark pH was measured in bark samples: 0.5 g air dried bark was mixed with 5 ml distilled water, the samples were left over night and pH was measured (Metrohm 744 pH Meter). Bark moisture was measured with a moisture meter (Protimeter Digital) and soil moisture was estimated in five moisture classes (Anonymous 1996) in a 2 m radius zone around each host tree.

RGR was regressed against precipitation, and colony growth rate was modelled from RGR at the mean precipitation 1961-1990. Ages of the colonies were estimated from the model.

Field study of *Buxbaumia viridis*

A field study was conducted to investigate the metapopulation dynamics of *B. viridis*, as affected by habitat quantity, habitat quality and precipitation (**I, V**). Two forests were surveyed in October-November 1996 and all findings of *B. viridis* were noted. In May 1997 a total of fourteen permanent plots of 25 x 25 m were established. The plots were positioned to include different densities of occupied patches. In October and November 1997-2003, the plots were searched for sporophytes. The numbers of mature sporophytes were counted in June the following year. From 1999 onwards, the plots were extended with a 10 m zone surrounding the original plots, where all patches occupied by *B. viridis* were recorded. A patch was denoted as occupied if at least one sporophyte was formed on it.

In the 25 x 25 m plots, all wood patches >10 cm in diameter and those with a diameter between 5 and 10 cm having a length of >50 cm, were mapped. For each wood patch the following was noted: number of sporophytes of *B. viridis* (individually marked), x- and y-coordinates in the plot, diameter and length of logs and stumps, suitable patch area, stage of decomposition following Söderström (1988b), wood taxon (*Picea abies*, *Pinus sylvestris* or deciduous) and softness of the softest and hardest parts of the wood. Softness was measured as the depth to which an 18 cm long pointed steel-rod with a diameter of 2 mm could be pushed into the wood. Further, it was noted whether the wood was very dry and if it was completely covered by terricolous bryophytes. Suitable patch area constitutes only the part of each patch with a potential to house *B. viridis*, and was estimated with experience from earlier findings of the species. Fairly moist bare wood, wood with algae or with a sparse cover of liverworts (mostly *Chiloscyphus profundus*) or small shoots of mosses (e.g. *Herzogiella seligeri, Brachythecium oedipodium*, *Hypnum cupressiforme*, *Aulacomnium androgynum, Pohlia nutans)* were regarded as suitable.

Decomposition of the wood is a continuous variable which practically has to be measured as a class variable. In this thesis I have used the eight decomposition classes as compiled by Söderström (1988b): 1.Wood hard, bark remaining intact. 2. Wood hard, bark broken up in patches but more than 50% remaining. 3. Wood hard, less than 50% bark remaining. 4. Wood has started to soften, without bark, texture smooth. 5. Wood soft, with small crevices and small pieces lost. 6. Wood fragments lost so the outline of the trunk is deformed. 7. The outer surface of the log is hard to define, possibly with a core of harder wood. 8. Completely soft without evidence of hard wood, outline indeterminable. The average transfer between classes is approximately linear over time (Naesset 1999; Jonsson 2000; Kruys et al. 2002) and in simulations of metapopulation dynamics (**V**) the decomposition classes were treated as a continuous.

Metapopulation simulations

Using the results from the field study described above, a spatially explicit patch occupancy model was constructed to simulate metapopulation dynamics of *B. viridis* (**V**). The model consisted of five sub models: decomposition of wood, precipitation, extinctions, colonizations and formation of sporophytes (Fig. 2). The simulation started with the data of separate wood patches as measured in 1997 and simulations were made with a time step of 1 year. Precipitation between May and October was randomly drawn from a normal distribution with a mean of 315 mm and a standard deviation of 76 mm, calculated from precipitation data 1940-2003 (Fig. 1). To avoid unrealistic values, precipitation was not allowed to be lower than 138 mm or higher than 530 mm, which is 10% lower and higher than the lowest and highest values measured between 1940 and 2003 (range 153-481 mm). The rate of decomposition was based on a complete decomposition time of a *Picea abies* log of 65 years, approximated from Hytteborn and Packham (1987). In each time step, probabilities for colonizations and extinctions were calculated using logistic regression models which were parameterized from field data. Unoccupied patches were tested for colonization, and occupied for extinction, by comparing the calculated probabilities with a uniformly distributed random number between 0 and 1

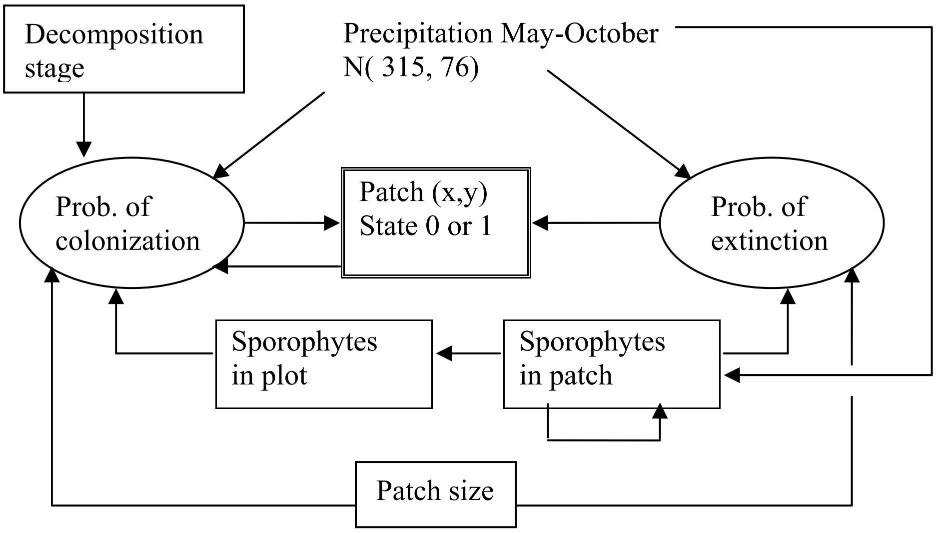


Fig. 2. Schematic illustration of the metapopulation model. The calculated probabilities of colonization and extinction were compared with a uniformly distributed random number between 0 and 1. Unoccupied patches were tested for colonization, and occupied for extinction. Time step is 1 year.

(Sjögren-Gulve & Ray 1996). Only one state transition was allowed per time step. Numbers of sporophytes formed on each occupied patch were estimated with a Poisson regression model parameterized from field data.

The simulations were made separately in the fourteen plots and to estimate total number of occupied patches in the forests, the surveys of the whole forests in 1996 was used. The number of occupied patches in the plots was multiplied by the ratio between number of occupied patches in whole forest and number of occupied patches within the plots. These ratios were 3.000 and 1.364 in the two forests.

To examine the dynamic of the species over time, the size of a metapopulation was simulated over 200 years, with a stochastic precipitation. To investigate the effect of reduced quantity of dead wood in the forests, a comparison was made between the intact forests and the same forests with a reduction of 50% of dead wood patches, simulated over 100 years. Since *B. viridis* was common in both the studied forests, the modelled effect of sporophyte density within the plots was not strong enough to extirpate the metapopulation for ever. None of the studied patches were recolonized after more than three empty years, I therefore considered a metapopulation as extinct after four consecutive years with no occupied patches.

Statistical analyses

All statistical analyses were made with SAS Software Release 8.2 (SAS 2001). The effect of the different treatments on germination of spores were analysed using linear (**II, III**) or logistic regressions (**III**). The effects on protonemal growth (**II, III**) were analysed using linear regressions. Analyses of covariance were used in several papers, e.g. to evaluate differences between chemical properties of dead wood in different decomposition classes (**II**), differences between wood of *Picea abies* and deciduous species in suitability for *B. viridis* (**I**) and the response of a species to precipitation (**I, IV, V**). Poisson regression was used to model number of sporophytes of *B. viridis* formed on occupied patches (**V**). When necessary, variables were transformed to improve homogeneity of variances and achieve normally distributed residuals.

Relative growth rate in colonies of *N. pennata*, as affected by microhabitat factors, competition and precipitation was analyzed using a mixed linear model with repeated measurements (**IV**).

Probabilities of establishment on substrates with different qualities were modelled in three ways: (1) by comparing differences between patches occupied and unoccupied of *B. viridis* using logistic regression (**I, V**), (2) by analysing pH, nitrogen and phosphorus concentration in dead wood patches with and without sporophytes of *B. viridis* (**II**), and (3) by constructing logistic and linear models from parameters in cumulative germination curves obtained from cultivation experiments (**III**).

The comparison of quality of dead wood with and without occurrences of sporophytes was tested using logistic regressions. The wood sampling was done as a case (occupied patches)/control (empty patches) study and hence, inferences about the intercept parameter were not possible. However, the odds ratios are invariant of study design (Hosmer & Lemeshow 1989) and they were used to compare probabilities. The odds ratio estimates the chance of having sporophytes at a certain pH, P or N, compared to having sporophytes at a specified pH, P or N. The odds ratios were calculated as:

$$\frac{\text{occupied at } A_i \times (\text{empty at } A_i)^{-1}}{\text{occupied at } A_s \times (\text{empty at } A_s)^{-1}} \qquad \text{equ(3)}$$

where A equals the measured variables pH, P, N or moisture, i corresponds to different values of the variables and s corresponds to a specified value of pH, P, N or moisture to which the odds of i was related. The specified value of s was set to the first quartile of frequency distribution. Odds ratio at this point equals one.

Cumulative germination curves were modeled by the Gompertz growth model (Draper & Smith 1998)

$$\omega = \alpha \exp(-\beta e^{-kt}) \qquad \text{equ (4)}$$

where ω is cumulative germination at a given time and t is time in days from the start of cultivation. The parameters α, β and k were estimated from the datat by non-linear regression, where α represents the final cumulative germination. The parameters β and k were used to calculate the time to germination of 2% of the spores (t_2) and to 50% of the final cumulative germination (t_{50}). The value of t_2 was interpreted as the lag phase before the start of spore germination; t_{50} is the time taken for the average spore to germinate and the difference between t_{50} and t_2 (Δt) was used to evaluate the rate of germination. The Gompertz model was used because it is not symmetrical about its point of inflection and the cumulative germination rate was faster in the first 50% fraction of the spores than in the second.

Results and discussion

The importance of moisture, pH and nutrients for spore germination

The chemical quality of the substrate was very important for spore germination of both *B. viridis* and *N. pennata* (**II, III**). Establishment of *B. viridis* from spores increased with increasing phosphorus, but not nitrogen, concentration in the cultivation media (**II**). Moss spores are small, generally only 10-30 µm in diameter (Boros & Járai-Komlódi 1975) and carry minor amount of nutrients. Hence, it is possible that external minerals is of significant importance for successful establishment. That phosphorus, and not nitrogen, is the limiting element for establishment from spores has also been observed in different *Sphagnum* species (Boatman & Lark 1971; Sundberg & Rydin 2002).

Although *B. viridis* inhabits acid and *N. pennata* base-rich substrates, germination success increased with increasing pH in both species. However, *B. viridis* was less sensitive to low pH than *N. pennata* when water was freely available (Fig. 3 left panel). In nature, however, periods with unlimited water availability is often short, and germination restriction at low pH was much more pronounced at reduced water availability (Fig. 3 right panel). There was a strong interaction between pH and water potential in prediction of the final cumulative germination: the spores reacted positively to one factor only when the other factor was in a favourable range (Fig. 4).

Bark is prone to desiccation, and germination depends on temporary 'windows of opportunity', i.e. short wet periods when spore germination is possible. In this aspect, the quality of the substrate becomes exceedingly important. Increased pH (1) increased the number of spores that finally germinated, (2) reduced the lag-phase (number of days) preceding germination, (3) increased the cumulative germination rate, (4) increased the protonemal growth rate, and, not the least, (5) made germination possible at lower substrate moisture (**III**). The last mentioned effect prolongs the temporary windows of opportunity, and might be of large ecological importance. A fast germination process might be ecologically important, since slow spore germination increases the risk of desiccation or disappearance of the spores

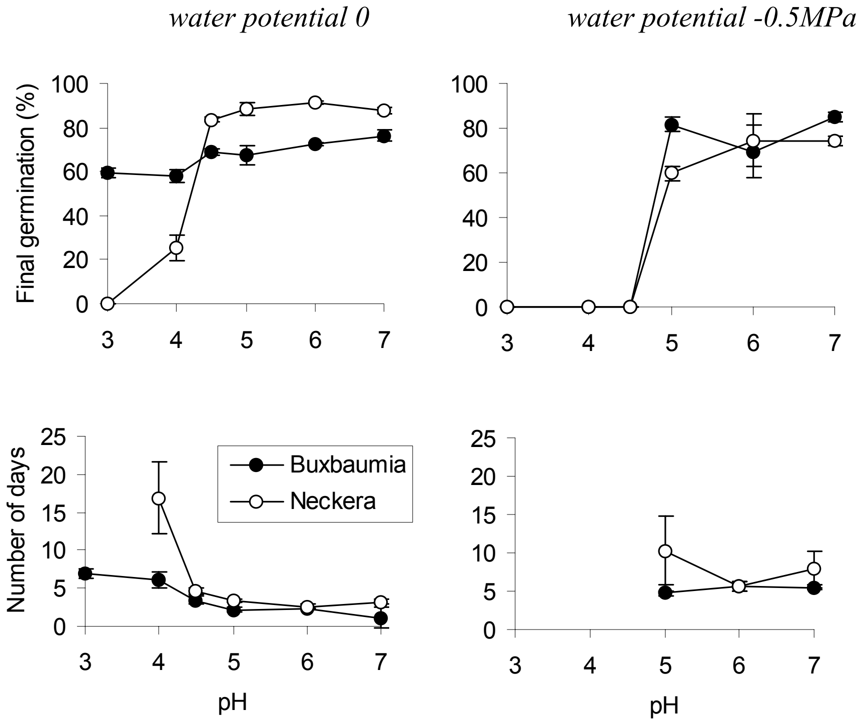


Fig. 3. Germination success expressed as fraction of spores finally germinating (upper graphs) and number of days preceding start of germination (lower graphs) at unlimited water (left) and reduced water availability (right). Error bars denote standard error. Data from paper **III**.

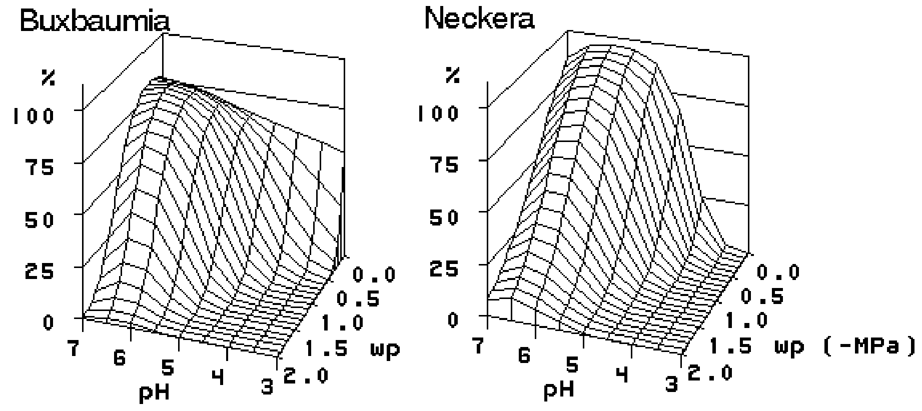


Fig. 4. Fraction of spores finally germinating (%). Data from paper **III**.

by wind or predation. Altogether this might explain why *N. pennata* is rare on trees with pH<5.5 (unpublished data Swantje Löbel).

Wood in late stages of decay remain wet for some period after rainfall due to the high water holding capacity of well decayed wood and because of the conversion of cellulose to metabolic water during the decomposition process (Rayner & Boddy 1988). However, during periods with little rain the dead wood dries out, and also the epixylic species might take advantage of temporary windows of opportunity. The importance of substrate phosphorus and pH found in the cultivation experiments was supported by a field investigation of *B. viridis*. As an example, increasing pH from 3.88 to 5.0 increased the probability of having sporophytes by 4.8 times (**II**). Further, the field study indicated that both germination and protonemal growth of *B. viridis* required an input of phosphorus beyond precipitation. This may be supplied either from the substrate, from litter accumulated on the wood or from throughfall.

The results from the spore establishment experiments reflected the habitat of the species, which supports the notion that bryophytes are most affected by substrate quality during the establishment stage (Brown 1982; Bates & Bakken 1998). A relationship between pH of the natural habitat and establishment success in cultivation experiments has also been observed in other mosses (Cameron & Wyatt 1989; Bosley et al. 1998).

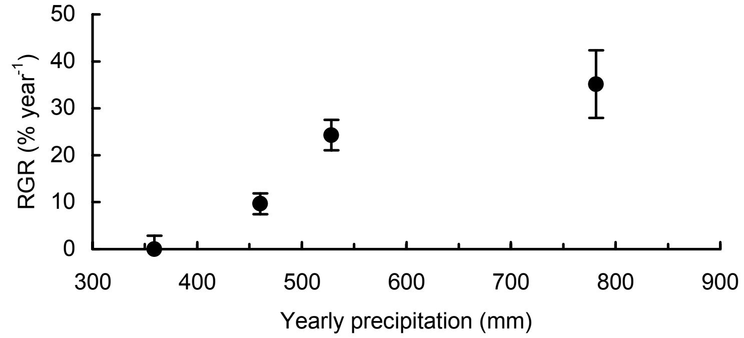
Although *B. viridis* and *N. pennata* inhabit contrasting microhabitats, and responded differently to the treatments, there was a common general pattern for both species. The three-dimensional plots of final germination percentage vs. pH and water availability (Fig 4) clearly show a split between a tenable and an untenable region of the response surface. In paper **III**, we suggested a general trade-off between the ability of moss spores to colonize substrates with low moisture holding capacity and low pH. This means that substrates prone to fast desiccation, such as the bark of living trees, should be colonised only if they have a fairly high pH. Substrates with a high water-holding capacity, such as wood in late stages of decay, or peat, could be colonised despite low pH.

Precipitation, microhabitat and competition

Since bryophytes lack roots, precipitation is a very important source of both nutrients and water. Growth of *N. pennata* (**IV**) and sporophyte formation (unpublished data) as well as patch occupancy (**V**) of *B. viridis* were highly affected by precipitation (Fig. 5).

Precipitation was clearly the most important predictor of relative growth rate (RGR) of *N. pennata*. Correlations between growth and precipitation has

Neckera pennata



Buxbaumia viridis

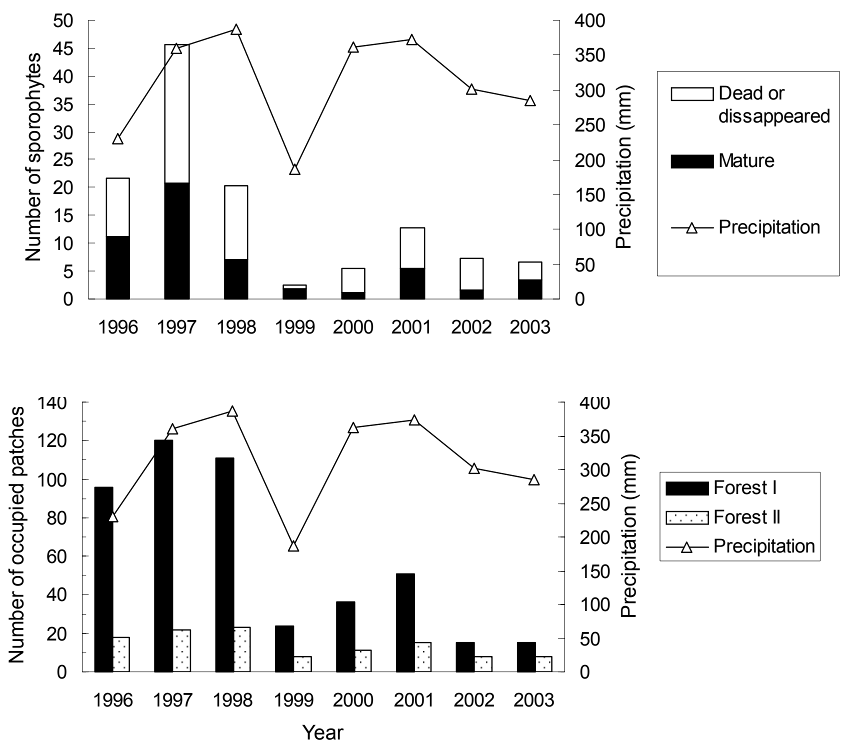


Fig. 5. Illustrations of the importance of precipitation on relative growth rate (RGR) in *N. pennata* (above), on formation of sporophytes (middle) and patch occupancy (below) in *B. viridis.* Number of sporophytes is given per 25 x 25 m plot as mean value of both forests. Number of occupied patches is given per forest (20 ha in forest I and 6 ha in forest II). Precipitation refers to the sum of May-October. Data from paper **IV**, **V** and unpublished**.**

earlier been observed in several other bryophytes (Tallis 1959; Pitkin 1975; Busby et al. 1978; Backéus 1988; Vitt 1990). Considering the interaction with precipitation, increased tree diameter had a negative effect on growth, while increased bark moisture and height position on stem (range 10-173 cm) had a positive effect. Cover of other epiphytes surrounding the colony had a negative impact on growth of *N. pennata*. The negative effect of cover of other epiphytes were interpreted as interference competition (Rydin 1997) and when this effect was strengthened, by exclusion of some small neighbouring species, tree diameter and height on stem were no longer significant variables. I interpret this as that competition was higher on larger trees and at lower positions of the trees, and that the reduced growth at these positions was an effect of competition. This is in agreement with a study of four epiphytes, in which *N. pennata* avoided the lowest 0.5 m of the stems, but showed the same response of photosynthesis and respiration to drying as the species growing there (Tobiessen et al. 1979). An alternative explanation would be that growth was restricted at its lower position by light, which has been observed in other trunk species (Hosokawa et al. 1964), but this seems less likely to me. Increased bark moisture had a positive effect on growth, but bark pH (range 5.4-7.9) or tree species did not affect the colony growth. Neither was there any correlation between cover of *N. pennata* on a tree and the colony growth (**IV**). This implies that precipitation and competition were the main factors affecting colony growth, and that the quality of the substrates, except for the moisture holding capacity, were of less importance. Thus, it is probable that occurrence was limited by establishment and that the species therefore is restricted to high quality trees.

Sporophyte formation in *B. viridis* and number of stumps or logs occupied by the species, showed the same pattern in relation to precipitation (Fig 5 middle and below). The fraction of formed sporophytes which succeeded to maturity, varied among years between 22 and 69% in forest I, and between 21 and 90% in forest II, with a mean of 43% over both areas and all years (unpublished data).

B. viridis showed a clear preference for dead wood characterised by loss of wood fragments and a partly or wholly deformed outline of the log or stump (**I**). Further, occupancy was favoured by high softness of the softest part of the wood patch. These properties arise in dead wood in late stages of decay as well as in humus. Typical for such substrates is the high moisture holding capacity. However, despite its lower moisture, *B. viridis* was occasionally found on bark of coarse woody debris of early decomposition stages, and those occurrences might be explained by the higher pH and nutrient concentration in bark compared with wood. Occupancy was negatively affected if the softness of the hardest part was high, which occurs in the very late stage of wood decay and probably is an effect of competition from terricolous bryophytes such as *Hylocomium splendens*, *Pleurozium schreberi* and *Rhytidiadelphus triquetrus.*

Modelled growth rate of *Neckera pennata*

The modelled area expansion of *N. pennata* was very slow (**IV**). Average RGR, assuming a precipitation of 544 mm year^{-1}, was 18.2% year^{-1}. Ten years after spore germination the modelled colony size was only 2 cm^2, it took 19 years before the colony exceeded 10 cm^2 and 31 years before it reached a size of 100 cm^2. The RGR model was applied to four sites, where all trees earlier had been searched for *N. pennata*. The annual colonization rate as calculated from colonies 11-35 years old (acknowledging that younger colonies may be overlooked and that tree number in the sites was constant) was 1.3%. Snäll et al. (2004) observed a colonization rate of 1.8% per year in populations of *N. pennata* within the same sites. However, it is important to remember that both colonization and growth are highly sensitive to precipitation and that large variation exists between years.

In the investigated sites, *N. pennata* had a colony size of 12-79 cm^2 when sporophytes were formed for the first time. According to the growth model this corresponds to an age range of 19-29 years.

Life history strategies

Bryophytes have been classified into different life strategies based on type of reproduction, reproductive effort, size and number of spores, annual production and life expectancy (During 1979;1992). According to this classification *B. viridis* is a typical colonist, with a short life span and many small spores. For dispersal between patches *B. viridis* relies completely on spores. One might think this should be a problem, since *B. viridis* is dioicous and adjacent male and female protonemata are necessary for fertilization and sporophyte formation. However, when fertilization is successful, each capsule will contain several millions of spores (**I**) and possibly they are not randomly, but wind direction dependently, dispersed, and many spores might land within a couple of cm. In this thesis I have denoted a patch as occupied if at least one sporophyte was formed on it (**I, II, V**). Although it is possible that the species is more common than is presumed from sporophyte occurrences, this is the only practical alternative. I justify it by the fact that only the sporophytes can contribute to the persistence of the metapopulation; in patches and forests with only single protonemata, the species will rather soon be extinct.

Nevertheless, it would be interesting to understand how common the gametophytes are. Duckett et al. (2004) concluded that the protonema of *B. viridis* is morphologically very distinct, with colourless sparsely branched rhizoids and once-branched somewhat undulating chloronemal filaments, impossible to confuse with associated species. In cultures of *B. viridis* I have, however, observed several-branched protonemata and also a frequent fuse of different protonemata (**II**), a phenomenon also noted in *B. aphylla* (Dening 1928). This capacity of protonemal fusion is interesting and could perhaps contribute to nutrition of the sporophytes. Another character which can be used to identify gametophytes of *Buxbaumia* is the unique formation of gametangia directly on protonemal branches. The brown antheridia are easy to recognize.

Protonemal growth of *B. viridis* was slow; the mean diameters in different treatments were only 0.5-3 mm, after 70 days of cultivation (**II**). Unlike some other bryophyte species colonising bare surfaces (Dening 1928; Dietert 1979; Lloret 1991) protonemata of *B. viridis* do not seem to expand quickly to cover empty wood surface.

N. pennata is also restricted to a patchy and dynamic habitat. However, living tree stems are much less dynamic and more long-lived than decaying wood, and although *N. pennata* has to disperse to new trees to persist in the landscape, this process can be slower than in *B. viridis*. *N. pennata* shows characteristics of a perennial shuttle species (During 1979): long life-span, high age of first reproduction and large spores. Such species typically occupy stable habitats which predictably disappear after a certain period. The long estimated pre-reproductive period of 20-30 years (**IV**) can perhaps be explained by a high costs of reproduction (Ehrlén et al. 2000) or simply by morphological constraints; sporophytes are formed on secondary decumbent shoots, which in my study were at least 3 cm long when sporophytes were formed. Many epiphytes commonly inhabit calcareous rock or on boulders in deciduous forests, but *N. pennata* are very rarely found on rock (personal observations, Nyholm 1979a; ECCB 1995). This is interesting, and an answer to why this is so, might be found in a combination of establishment problems and the slow growth of *N. pennata* (**IV**). However, this requires further studies to fully understand.

Metapopulation dynamics of *Buxbaumia viridis*

In the metapopulation analysis of *B. viridis* (**V**), a patch was denoted as occupied if at least one sporophyte was formed on it. Of the 87 patches occupied at least one of the eight years of study, 26 were temporary occupancies of only one year (Fig. 6a). On the occupied patches, normally less than 5 sporophytes were formed (Fig. 6b). Since metapopulation sizes decreased during the investigated period (Fig. 5), the number of extinctions (n = 106) exceeded the number of colonizations (n = 54). Of the colonizations, 43% corresponded to patches that had not been previously occupied during the study period while 57% were recolonizations. Of the recolonizations the most common pattern was a recolonization after one empty year. No recolonization occurred after more than three empty years. Precipitation, as measured as sum between May and October was the most important variable, affecting probability of both colonizations and extinctions. Although the high influence of precipitation on occupancy resulted in synchronous popu-

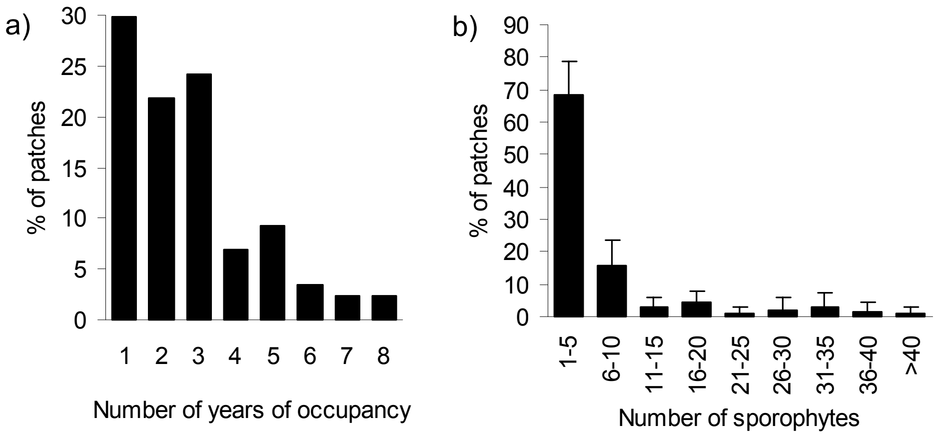


Fig. 6. a) Total number of years, out of eight, in which sporophytes of *Buxbaumia viridis* where found on each wood patches within the plots, n = 87 patches.
b) Number of sporophytes found on occupied patches given as mean and standard deviation among years (1996-2003).

lation dynamics, *B. viridis* clearly showed metapopulation characteristics. Extinctions of local populations were widespread and colonizations must balance them for persistence of the total population. The risk for extinction was decreased by a large population size in the previous year, and by a large patch size. This is in accordance with classical metapopulation theory (Hanski 1998). The probability of colonization increased with increasing patch size, which is not surprising given that *B. viridis*, like most bryophytes, is passively dispersed by wind. Hence, the probability to find a suitable site for establishment increases with increasing patch size. Patches are rarely equally suitable, and including habitat quality in metapopulation models usually improves model fit (Verboom et al. 1991; Moilanen & Hanski 1998; Fred & Brommer 2003; Johansson & Ehrlén 2003). Patch quality, represented by decomposition class, did also affect the probability of colonization. Occupancy during the three years preceding the empty year was an important variable explaining colonization, or in fact recolonization. Also connectivity, measured as number of mature sporophytes in the plots in the previous year, had a positive effect on colonization

Simulating occupancies over 200 years, using stochastic precipitation drawn from a normal distribution, revealed a highly fluctuating metapopulation (Fig. 7). During periods with a precipitation above mean for several consecutive years, as between year 80 and 91, or during a long period with few years with precipitation much below mean, as between year 131 and

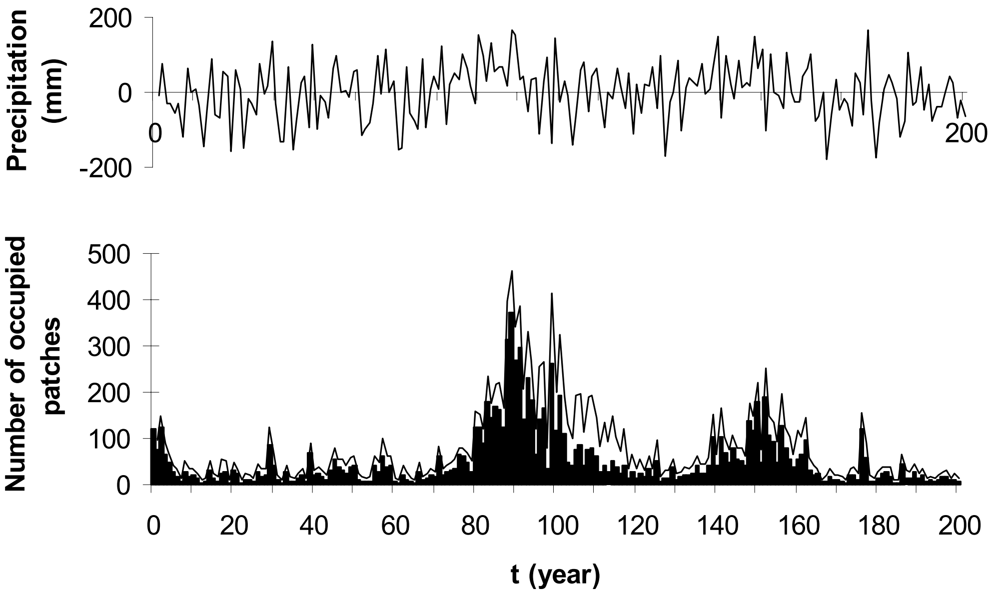


Fig. 7. Fluctuations in a metapopulation of *B. viridis*. The lower graph shows number of occupied patches in a 20 ha forest, mean (bars) and upper 2.5 percentile (line) of 50 replicated simulations. The upper graph shows deviation from normal precipitation (315 mm) in May-October, randomly drawn from a normal distribution. Data from paper **V**.

162, the population size could successively increase to very high numbers.

Reduction in quantity of coarse woody debris by altered forest management is one of the most obvious and important changes in boreal forests in the 20th century (Kirby et al. 1991; Östlund et al. 1997). For that reason, I simulated a reduced number of wood patches by 50% in both forests. The effect was a decrease in mean number of occupied patches, but the occupied fraction of patches remained the same as before patch reduction. However risk for metapopulation extinction increased seriously in the smallest of the two forest areas (Fig. 8).

Both field data and simulations demonstrated that metapopulations of *B. viridis* were highly fluctuating, which is to be expected when correlated environmental stochasticity has a large impact on the populations (Moilanen 1999). Larger impact of correlated environmental stochasticity than of demographic stochasticity has been predicted for large metapopulations (Harrison & Quinn 1989; Lande 1993) unless dispersal between patches is very high (Hanski 1989). My result emphasizes the importance to take environmental factors, e.g. precipitation or temperature, into account, in analyses of population dynamics.

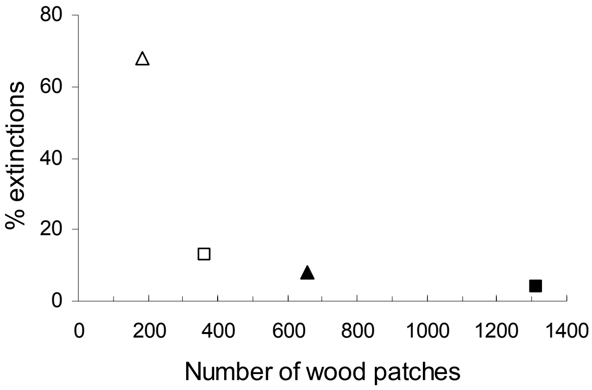


Fig. 8. Predicted number of extinctions of whole metapopulations within 100 years, using original number of patches (squares) or a reduction by 50% of number of patches (triangles). Number of wood patches refers to the quantity in two forests of different sizes: Forest I (open symbols) 20 ha, and forest II (filled symbols) 6 ha. Each scenario was simulated 100 times with different random precipitation sequences. Data from paper **V**.

Implications for conservation

B. viridis and *N. pennata* are two species with very different life strategies and habitats, but both depend on substrates which have decreased as a result of an intensified forestry. Reduced amount of substrates is thus a basic explanation to the supposed decline of the species (ECCB 1995). However, all species inhabiting decaying wood and deciduous tree trunks are not threatened, and in this thesis I have tried to elaborate on how establishment constraints, growth and metapopulation dynamics might affect the rarity of the two studied species.

Because of the restricted life span of the substrates, establishment is probably a key-process. Although *N. pennata* most likely can establish from shoot fragments, it does not have any specialized asexual diaspores. Hence, both species are probably dispersed by spores. For establishment from spores, substrate quality seems to be of crucial importance; increased quality results in increased probability for successful establishment.

The substrate of *B. viridis* has a high water holding capacity, and its quality can be improved by increased pH and phosphorus availability (**II, III**). This might be achieved by litter and throughfall form deciduous trees standing close to patches of dead wood. Although germination and protonemal growth were favoured by increased water availability in cultivation experiments (**III**), *B. viridis* would not necessarily benefit from increased wood moisture, because in nature it might be outcompeted by species with higher capacity to take advantage of the increased moisture.

The large fluctuations in population size of *B. viridis* (**V**) are a threat to its persistence, especially in small forest areas. To buffer this, large metapopulations which will remain also during climatically bad years, are essential.

The substrate of *N. pennata* is prone to desiccation, and germination and protonemal growth are most likely limited by water. On such substrates the length of the period when germination is possible, the 'window of opportunity', has high impact on the germination probability. The strong interaction between pH and moisture (**III**) on germination implies that the quality for establishment can be increased either by prolonged wet periods or by increased substrate pH. Acid deposition decreases bark pH and hence, lower the probability of establishment, which might explain why several epiphytic bryophytes have declined (Hallingbäck 1992; Sjögren 1995). Thus, *N. pennata* would benefit from higher soil moisture, more base-rich deciduous trees and increased pH in precipitation. The slow growth and late reproduction

(**IV**) of colonies might also contribute to the rarity of *N. pennata* since this implies that the colonization process in the forest is initially very slow.

Both *B. viridis* and *N. pennata* have a southern and eastern distribution focus in Sweden (Hallingbäck 1998), which means less precipitation and less acid deposition than in the western parts. Both species were negatively effected by surrounding bryophytes (**I, V**), and it is possible that the two studied species are excluded by competitors on the most suitable patches in western parts of Sweden. The distribution of *B. viridis* in Sweden (Hallingbäck 1998) seems to be more related to forests with high cover of deciduous trees, as inferred from distribution maps of cambisols (Nilsson 1990), than to areas with high precipitation. In Norway *B. viridis* shows preferences for rich forests (Blom et al. 2001).

To sum up, the abundance of species restricted to patchily distributed substrates of limited duration is influenced by substrate quantity, substrate quality, connectivity between habitat patches and interactions with competitors. Further, the substrate quality and the effect of competition are influenced by environmental factors such as quantity and quality of precipitation, and forest type. Altogether this forms a complex network where probabilities of diaspore transport, establishment, growth and reproduction determine the success of the species.

Acknowledgements

During the work with this thesis I have learnt two main things: to think like a scientist and to think like a bryophyte, and I have really had great fun. For this I am indebted to a lot of people and to two mosses. Håkan, I truly appreciate your support. Without your supervision this work would never had come to an end (what I don't understand is how you could be as cool as a cucumber when nothing succeeded and time always seemed too short). Håkan has made very large improvement in all papers; he also suggested the study in paper IV.

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Finally, what about the two bryophytes? Have you ever tried to draw something on a plastic sheet in a forest in the autumn? The air is humid, the temperature is low and the tree stems are still moist - the color from your pen does not stick to your plastic sheet. Of course you get annoyed, but you also realize that, if you are an epiphytic bryophyte, this is your ‘window of opportunity’.

Major financial support for the studies of *Buxbaumia viridis* was granted from World Wide Fund for Nature (WWF). The studies in the thesis have also been financially supported by Formas and by scholarships from Extensus, Sernanders, Växtgeografiska sällskapet and The Royal Swedish Academy of Sciences.

Etablering, tillväxt och populationsdynamik hos två mossor som signalerar skyddsvärda skogar

Mossor är viktiga för den biologisk mångfalden i skogar

Mossor står för en väsentlig del av artmångfalden i svenska skogar. På rödlistorna över hotade arter finns idag 238 mossor och av dem förekommer 102 i skogen. Det intensiva skogsbruket har lett till mindre andel gamla skogar, färre ädellövbestånd och generellt torrare skogar. För att vi ska kunna behålla ett artrikt skogsekosystem är det viktigt att vi får större kunskaper om olika mossors ekologi och hur vi bäst bevarar dem. De flesta skogsarter av mossor växer inte på marken, utan på olika substrat som stenblock, död ved och trädstammar av lövträd.

Grön sköldmossa och aspfjädermossa

Grön sköldmossa (*Buxbaumia viridis*) och aspfjädermossa (*Neckera pennata*) är två av de arter som används som indikatorer på skyddsvärd skog. Grön sköldmossa finns i stort sett bara på död ved och indikerar rik tillgång på sådan. Aspfjädermossa växer på stammar av lövträd och indikerar äldre skogar med kontinuerligt inslag av gamla lövträd. Bägge arterna är rödlistade, både i Sverige och i Europa. Grön sköldmossa finns dessutom med som en av 30 mossor i EU:s habitatdirektiv. I Sverige har arterna en sydlig utbredning och är vanligare i de östra delarna.

Jag har undersökt ekologin hos grön sköldmossa och aspfjädermossa genom att studera arternas sporgroning under olika betingelser, mäta tillväxten hos aspfjädermossa på träd i naturen och genom att följa utvecklingen av grön sköldmossa i två skogsområden under åtta år.

Etableringen är en nyckelprocess

Död ved och levande trädstammar är substrat med begränsad livslängd. För arter som lever på sådana substrat är spridningen till nya växtplatser, och en framgångsrik etablering på dessa, helt nödvändig för att arterna ska finnas kvar i ett område. Etablering av grön sköldmossa och aspfjädermossa sker troligtvis från sporer och jag har studerat hur dessa gror vid olika pH, kvävehalt, fosforhalt och vattentillgänglighet.

Trots att det naturliga substratet för grön sköldmossa har ett lågt pH medan substratet för aspfjädermossa har högt pH, reagerade bägge arterna positivt (fler sporer grodde) på en höjning av pH i näringslösningen. Vid låga pH-värden kunde arterna bara gro om det samtidigt hade hög tillgång på vatten. Hur högt pH-värdet var hade också betydelse för hur lång tid det tog för sporerna att börja gro, vilket kan ha stor betydelse i naturen eftersom sporerna bara kan gro när substraten är fuktiga.

I ett odlingsexperiment med grön sköldmossa visade det sig att den, förutom förhöjt pH, också reagerade positivt på ökad tillgång på fosfor. Detta är intressant eftersom fosforhalten i nederbörden är låg.

Det tar lång tid innan aspfjädermossa börjar bilda sporer

Under tre år studerade jag 81 kolonier av aspfjädermossa och det visade sig att de växte väldigt långsamt. Tillväxten var beroende av hur mycket det regnade, och under torra år växte de i stort sett ingenting alls. Med en tillväxtmodell beräknade jag åldern för när sporkapslar producerades för första gången till 20-30 år. Det tar alltså väldigt lång tid innan en koloni av aspfjädermossa bildar sporer som kan sprida arten till nya träd.

Det visade sig också att kolonier som växte på stora träd eller långt ned på stammen växte sämre. Troligtvis är detta en effekt av att konkurrensen från omgivande arter på trädet är högre på dessa ställen. Trädslag eller bark-pH hade ingen inverkan på tillväxten, vilket möjligen beror på att etableringsprocessen, inte tillväxten hos mossan, är begränsande för var arten förekommer.

Mängden sköldmossa varierar kraftigt mellan olika år

I två skogsområden placerade jag ut fjorton provrutor om 25 x 25 m och följde alla stubbar och lågor inom dessa under åtta år. Antalet stubbar och lågor där jag hittade grön sköldmossa varierade kraftigt mellan olika år. Detta antal var kopplat dels till hur många sporkapslar som producerades året innan, dels till nederbörden under maj till oktober under samma år. Populationerna på de flesta stubbar och lågor var kortvariga (tre år eller mindre), men på några enstaka överlevde arten under alla åtta undersökta år. För att undersöka hur mängden död ved i skogen påverkar artens förekomst, simulerade jag hur en minskad vedtillgång i de undersökta skogarna påverkade grön sköldmossa. Den största effekten var att sannolikheten för att arten skulle försvinna från ett litet skogsområde ökade dramatiskt

Vad krävs för att arterna ska finnas kvar?

Mängden död ved och lövträd med högt bark-pH har minskat kraftigt i våra skogar under 1900-talet och detta är troligen den största anledningen till den förmodade minskningen av grön sköldmossa och aspfjädermossa. Men mina undersökningar visar att även kvalitén hos substraten är viktig, framför allt för sannolikheten för att sporerna ska gro. Grön sköldmossa gynnades av förhöjt pH och ökad fosforhalt i veden. Arten gynnas därmed troligen i skogar med ett stort inslag av lövträd, vars förna och krondropp höjer pH-värde och fosforhalt på substrat i närheten. Grön sköldmossa var också betydligt vanligare på ved i sena nedbrytningsstadier, vilket sannolikt beror på den högre fuktigheten där. Fuktigheten får dock inte vara för hög, då blir konkurrensen från andra arter för stor.

Etableringen av aspfjädermossa skulle troligen gynnas av om barken behöll fuktigheten under längre perioder, t.ex. genom högre markfuktighet. Försurad nederbörd har möjligen haft en negativ inverkan på sporgroningen hos aspfjädermossa och en höjning av pH-värdet i nederbörden skulle kunna öka chansen för etablering.

Framgången för grön sköldmossa och aspfjädermossa, liksom för många andra arter som är beroende av död ved och lövträd, beror således på substratmängd, substratkvalité, avstånd mellan lämpliga växtplatser, mängden nederbörd och framgången hos andra konkurrerande arter

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