Clonal dynamics and evolution of dormancy in the leafy hepatic *Lophozia silvicola*

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Dead shoots of colonies of a leafy hepatic species, *Lophozia silvicola*, are replaced by shoots developing from asexual propagules, the gemmae. Observations of two populations of *L. silvicola* showed a strong decreasing seasonal trend in germinability of the gemmae. We suggest that the non-germinating gemmae enter dormancy, and that the proportion of gemmae entering dormancy is season-specific. We assume that there are two types of gemmae, dormant and non-dormant and that only the dormant gemmae can survive during winter. Using a stochastic individual-based cellular automaton model, we investigated whether selection on season-specific dormancy fraction would lead to a decreasing proportion of germinating gemmae. Thus the germination schedule is the evolving trait in the model. Parameter estimates for the model were based on data collected from a population of *L. silvicola* in southern Finland over a three-year study period. In the simulations, the germination schedule shaped by evolutionary change was similar to the observed pattern. Thus the modelling results give support to the dormancy hypothesis. The qualitative pattern of decreasing germinability towards the end of the growing season is robust. Quantitative predictions are influenced by changes in parameters; for example, if winter mortality of shoots increases relative to mortality during the growing season, production of an increased fraction of dormant gemmae is favoured, especially at the end of the season.

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Dormancy of propagules is widespread in both the animal and plant kingdoms, and it can play a crucial role in population dynamics. Dormancy has been considered as an evolutionary response to unpredictable environmental variability (e.g. Evans and Cabin 1995). Furthermore, dormancy and dispersal can be seen as alternative adaptations in temporally and spatially variable environments (e.g. Venable and Brown 1988, Cohen and Levin 1991, McPeek and Kalisz 1998). Generally, dormancy can be seen as a risk-spreading strategy that enhances survival, effective resource use and avoidance of competition in populations in temporally or spatially heterogeneous environments (Symonides 1989, Rees 1996, Hyatt and Evans 1998).

Most plant studies on dormancy have been made on vascular plants, where the ungerminated fraction of seeds forms a persistent seed bank in soil. In lower plants including bryophytes, dormancy of diaspores is less well known (Knoop 1984), although presence of spores or other propagules has been demonstrated in diaspore banks in chalk grasslands, arable lands and forest soil (During and Horst 1983, Jonsson 1993, Bisang 1996). In hepatic diaspores, dormancy has previously been reported in the thalloid species *Sphaerocarpos donellii*, *S. texanus* and *Blasia pusilla* (Kurz 1976, Duckett and Renzaglia 1993, McLetchie 1999). Harper (1977) distinguished two types of dormancy in plants: enforced dormancy with no germination because of

unfavourable conditions, and innate and induced dormancy with no germination even in favourable conditions without a specific stimulus required to break the dormancy. In bryophytes, survival of diaspores in the soil usually seems to be due to enforced dormancy, whilst the frequency of innate or induced dormancy is unclear (reviewed in During 1979, Mogensen 1981, 1983).

About 46% of hepatic species have been reported to produce asexual propagules at least occasionally (Laaka-Lindberg et al. 2000). Therefore, it is surprising that so little attention has been paid to dynamics and evolution of asexual reproduction in hepatics, even though its role has often been considered essential (Wyatt 1982, Mishler 1988; see also Anderson 1963). The topics of population dynamics and life history evolution of bryophytes have, however, been dealt with in a number of recent studies on mosses (e.g. Newton and Mishler 1994, Økland 1995, Hedderson and Longton 1995, 1996, Longton 1997, Rydgren et al. 1998). The few studies on population ecology of leafy hepatics include those by Jonsson and Söderström (1988, Söderström and Jonsson 1989) on *Ptilidium pulcherrimum*, and Laaka-Lindberg (1999) on *Lophozia silvicola*.

The importance of asexual reproduction becomes clear when considering the hepatic life cycle (Fig. 1) with alternating haploid (gametophytic) and diploid (sporophytic) generations (e.g. Schofield 1985). Gemmae are produced by mitotic cell divisions on leaves of the gametophyte shoot. Upon germination, a new juvenile shoot develops on a short protonemal tube in a similar fashion as in germinating spores, and this warrants the use of the concept of "asexual reproduction" in gemmiferous hepatics (see Mogie 1992). In species with facultative reproductive modes, sexual and asexual reproduction have different ecological and evolutionary roles (Newton and Mishler 1994), and in species inhabiting a system of habitat patches, randomly varying within-patch fitnesses favour propensity for both dispersal and dormancy (McPeek and Kalisz 1998).

Observations on natural populations of *Lophozia silvicola* in central Norway (Laaka-Lindberg 1999) and in southern Finland (this paper) have shown that germinability of gemmae decreases strikingly towards the end of the growing season. We put forward a hypothesis that some of the gemmae do not germinate because they have become dormant. If only the dormant gemmae can successfully overwinter, non-dormant and dormant gemmae will have different functional roles in clonal dynamics. Dormant gemmae can quickly colonise empty space created by shoot mortality during the winter, whereas non-dormant gemmae can replace the shoots that die during the growing season. Thus, the seasonal decline in germinability could actually be a consequence of an adaptive strategy, involving dormancy dependent on the time of gemma production.

In this paper, we first present field data on germinability and life history characteristics of *Lophozia silvicola* Buch, a leafy hepatic, which reproduces frequently by producing asexual uni- or bicellular gemmae in masses at the tips of the uppermost leaf lobes. *L. silvicola* is a dioicous species with separate female and male shoots. Frequency of sexually reproducing colonies is 16% ($n = 92$) in the sampling area. In contrast, asexual gemmae are abundant in all colonies. The data on life history characteristics are used to construct an individual-based model of clonal dynamics in this species. The model is used to investigate whether a seasonally increasing frequency of dormancy is a likely outcome of adaptive change in the ecological setting. Finally, the results of the model are compared with field observations of *L. silvicola*.

Materials and methods

Study site

The study site is a spruce-dominated old-growth forest in Kotinen Nature Reserve at Lammi commune, southern Finland (61°14′ N 25°03′ E). We sampled five colonies picked randomly in a 100-ha grid over three growing seasons from 1997 to 1999. The sampling was repeated in each of the colonies once a month during the growing season, from May to October. The data on production of gemmae and survival of shoots and gemmae are based on observations in the field and in the laboratory. The long-term averages of traits measured are used as parameter estimates in the individual-based model.
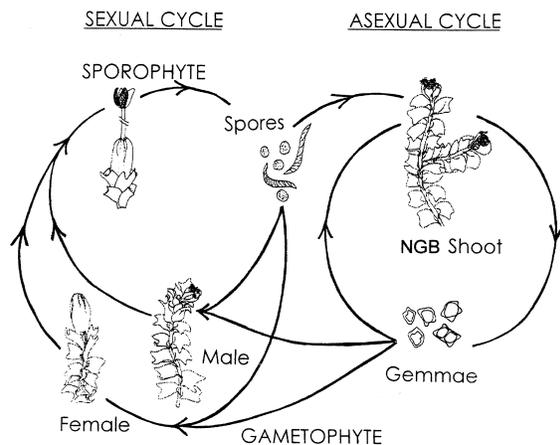

Fig. 1. Sexual and asexual reproductive cycles of gametophytes of *Lophozia silvicola*, and sporophyte generation as a result of sexual reproduction. Non-gametangia-bearing (NGB) shoots represent the mature gametophyte stage in the asexual cycle.

Gemmae counts, germinability and vitality

At each sampling time, we estimated the numbers of gemmae by counting the gemmae in a haemacytometer (Laaka-Lindberg 1999). As it was not possible to measure the production and release rates of gemmae directly in the field from the data on numbers of gemmae present on shoots, we made rough estimates of these parameters using an indirect method described in the section ''Model of the dynamics of *Lophozia silvicola*'' below. We tested the germinability of gemmae in Knop's liquid-culture medium (Nehira 1988) with the incubation time extended from two to three weeks (see Laaka-Lindberg 1999). Five replicates were used for each month's test. We estimated the vitality of dormant gemmae during the growing season 1999 by monitoring the state of non-germinated gemmae under a microscope after the three weeks incubation in the liquid-culture. Non-germinated gemmae with chloroplasts, intact cell walls and opaque cell contents were interpreted as being healthy, and the gemmae with transparent, deformed cells with contracted protoplasm as being dead.

Shoot survival and density

The survival of shoots over the winter and during the growing season was estimated by counting dead individual shoots in 1-cm² sample squares, assuming that shoots that died between sample times were still present, i.e. they had not decayed too much. The shoot density was measured in the same 1-cm² squares. The samples were collected from five colonies, divided into sectors sampled in a systematic sequence in order to avoid any effect of the destructive sampling on colony density. The sampling was repeated over the three-year period in the same colonies during the growing season. The proportion of living shoots in the first sampling in May was used to calculate an estimate of winter survival. To estimate the average colony size, we measured the surface area of all the *L. silvicola* colonies present on a 50 × 50-m sample plot.

The differences between sampling periods and between years in germinability, gemma production and shoot density were tested by ANOVA with repeated sampling design and Huyhn-Feldt statistics. Changes in germinability were further tested by a linear regression model. The tests were calculated using SYSTAT for Windows (1992) statistical software.

Field results

The average colony size of *Lophozia silvicola* in the sample area was 24.9 cm² ($n = 92$, S.D. 52.7). The average shoot density in the colonies was 21.0 shoots per cm² ($n = 18$, S.D. 5.55). No differences in shoot densities (Table 1) were detected, either between sampling months ($F = 1.210$, df = 5,10, $P = 0.372$, H-F = 0.372), or between years ($F = 0.475$, df = 2,10, $P = 0.635$, H-F = 0.635). Average monthly mortality of shoots (Table 1) in *L. silvicola* over the three years was fairly constant during the growing season, on average 3.5%. The proportion of dead shoots in the colonies was highest in the first sampling period, on average 13%, reflecting mortality in the preceding winter.

The average numbers of gemmae present on shoots during the growing season varied from 1088 to 2653 (Table 2). The difference between years was significant ($F = 9.845$, df = 2,10, $P = 0.004$, H-F = 0.004, Table 2), the three year average showing a slightly parabolic trend over the season (Fig. 2). The monthly averages are, however, not significantly different ($F = 1.824$, df = 5,10, $P = 0.196$, H-F = 0.196). At the start of the growing season in May, 69% of the gemmae germinated in the culture, and germinability decreased towards the end of the season to less than 20% (Table 1, Fig. 2). The linear regression model revealed a significantly decreasing trend in germinability through the growing

Table 1. Three-year mean values with S.D. of monthly shoot density, germinability of gemmae, and proportions of dead shoots, and dead gemmae in liquid culture of *Lophozia silvicola* used for model parameterisation.

	Sampling month					
	May	June	July	August	September	October
Shoot density						
Mean n/cm²	17.6	21.4	24.0	21.3	20.1	21.8
S.D.	2.35	2.30	4.62	1.51	2.17	4.47
Proportion of dead shoots; shoot mortality						
Mean proportion	0.13	0.038	0.037	0.028	0.040	0.032
S.D.	0.031	0.001	0.011	0.011	0.014	0.009
Germinability of gemmae						
Mean proportion	0.690	0.413	0.308	0.307	0.195	0.197
S.D.	0.132	0.184	0.065	0.121	0.039	0.027
Proportion of dead gemmae; gemma mortality						
Mean proportion	0.68	0.68	0.36	0.70	0.32	0.34
S.D.	0.252	0.171	0.371	0.228	0.068	0.079

Table 2. Numbers of gemmae present on shoots of *Lophozia silvicola* during the growing season from May to October over the three years of study. The monthly numbers of gemmae are mean values ($n = 5$) with S.D. Values in bold represent 3-yr average numbers.

		Sampling month					
		May	June	July	August	September	October
Y97	n/shoot	2130	2354	4391	3891	3781	1989
	S.D.	1680.6	876.5	2637.7	1371.3	4247.2	1393.8
Y98	n/shoot	533	1719	1417	1833	735	1016
	S.D.	480.8	976.5	2239.5	1505.0	3029.9	1138.9
Y99	n/shoot	602	787	1308	1333	3444	1384
	S.D.	515.8	775.3	556.0	875.7	1773.4	392.7
Y97-Y99	n/shoot	**1088**	**1620**	**2372**	**2352**	**2653**	**1463**
	S.D.	902.8	787.6	1749.4	1355.8	1670.4	491.3

season ($r^2 = 0.815$, $F = 17.639$, $P < 0.014$, Fig. 3). The proportion of dead, non-germinated gemmae varied between months (Table 1), being on average 51%.

Model of the dynamics of *Lophozia silvicola*

Model structure

We used an individual-based cellular automaton model (Judson 1994, Solé and Bascompte 1998) to model the dynamics of *Lophozia silvicola* in a patch. This is a suitable approach because patches are small, reproduction mainly asexual, gemmae are only dispersed locally and lack of space limits growth. We assumed that clones differ in the fraction of dormant gemmae produced during different parts of the season and that the type of gemma is influenced only by its mother's genotype. The variation in germinability is maintained by mutations that may occur in the gemmae. Evolutionary change in the model is driven by between-clone differences in ecological performance: competition occurs between the clones when gemmae germinate and replace dead shoots. The clones with high germination of gemmae at the times when replacement opportunities arise will contribute relatively many new shoots, and as a consequence these clones will increase in frequency.

Space was modelled as a square lattice, where each cell in the lattice supports at most one shoot, as well as an unlimited number of gemmae. The lattice size was 23×23 cells, corresponding to the typical size of a *Lophozia* colony in the field, 24.9 cm² with 21 shoots/cm². The growing season in the model was divided into the six months corresponding to the months of field sampling. The strategy of a clone is a vector of the probabilities that each newly produced gemma is non-dormant, p_i, $i =$ May, June, July, August, September, October.

At the beginning of each time step of the model, every mature shoot (at least 2 months old) releases a total number of f_i gemmae. The number of non-dormant gemmae released is a binomial variate with mean $p_i f_i$; the remaining gemmae enter dormancy. Half of the gemmae remain within the cell in which they were released; the other half are distributed uniformly randomly among the neighbouring eight cells. All gemmae that fall outside the lattice immediately die, whereas the others enter the diaspore bank. In the bank, dormant and non-dormant gemmae survive with monthly probabilities s_{ds} and s_{ns}, respectively. Shoots have a monthly survival probability s_{ss}. At the end of a month, empty cells are colonised by non-dormant gemmae through lottery competition (Chesson and Warner 1981). Only one gemma can take over the cell, and all other non-dormant gemmae in that cell die.

During the winter, all non-dormant gemmae die ($s_{nw} = 0$). Each dormant gemma has a survival probability s_{dw}, and each shoot has a survival probability s_{sw}. In spring, empty cells (i.e., without a shoot) are colonised by dormant gemmae from the gemma bank. A randomly chosen gemma becomes established as a new shoot, while all other gemmae in that cell die.
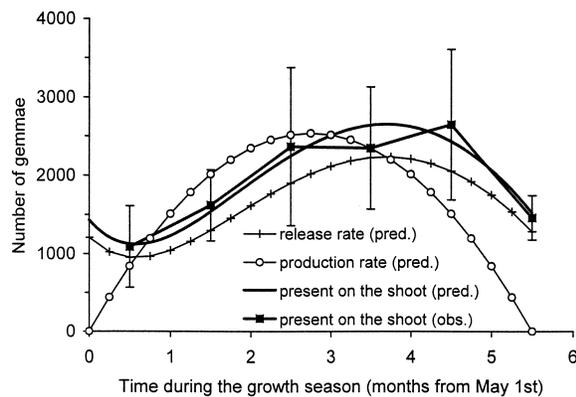

Fig. 2. Observed ($\pm$ S.E.) and predicted (see text for details) numbers of gemmae present on an average shoot of *Lophozia silvicola*. The model assumes a parabolic seasonal pattern in production of gemmae, and release of a constant fraction of the gemmae present at each time interval. Integration of release rate for each month gives the monthly numbers of released gemmae presented in Table 1.
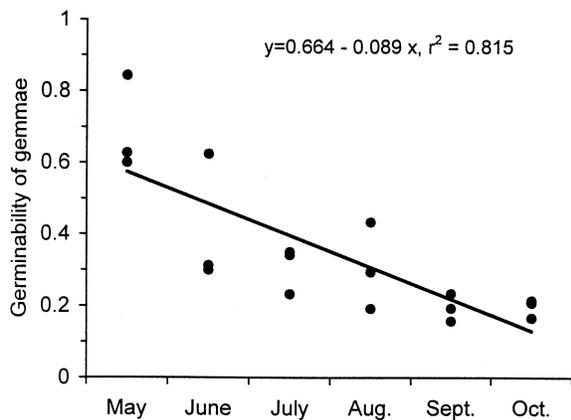
Fig. 3. Linear regression of germinability of gemmae in *Lophozia silvicola* along the growth season from May ($x = 1$) to October ($x = 6$). The decline in germinability is statistically significant ($F = 17.64$, $P < 0.014$).

The germination schedule was the evolving strategy in the model. This strategy was discretised such that probabilities of being a dormant gemma, p_i, can only have values 0, 0.25, 0.5, 0.75 and 1. Mutations occurred with probability $m = 0.01$ per gemma. The effect of a mutation was to change one of the dormancy probabilities p_i either up or down one step. Mutations that would have resulted in a value not in the range 0 … 1 were ignored.

Simulation procedure and parameter estimation

The simulations were initialised with one mature shoot with a germination strategy without dormancy placed into a randomly selected cell. The model was run for 1000 'years'. During this time, the population evolved to a stochastic equilibrium maintained by a mutation-selection balance, and the common clones were all similar to each other. At this stage, the coexisting clones formed an evolutionarily 'optimal' coalition in the sense that there was no directional selection for altered germination strategy. The last 200 yr were used to calculate mean population strategy, which we refer to as an 'evolved germination schedule'. The robustness of the results against uncertainty in parameter values was checked by letting parameters assume other feasible values. Below we introduce the default parameter values, henceforth referred to as the 'basic parameters'.

Survival probability of shoots during summer was estimated as the geometric mean of survival probabilities in June–October, obtained from the mortality values in Table 2. This yields an estimate $s_{ss} = 0.96$. Mortality observed in May (0.13) is assumed to be a result of within season mortality ($1 - s_{ss}$) and overwintering mortality. Thus we can estimate overwintering survival of shoots to be $s_{sw} = (1 - 0.13)/s_{ss} = 0.90$. The

fraction of dead gemmae is known from the germinability assays. However, dead gemmae are all alike, and we have assumed equal survival between the two types, $s_{ds} = s_{ns} = 0.70$. Overwintering survival of dormant gemmae cannot be known; here we assumed $s_{dw} = 0.50$.

No direct measurements of production and release rates of gemmae exist. However, using the data on actual numbers of gemmae present, we can obtain rough estimates by assuming that production of gemmae has a seasonal, parabolic pattern, and that a constant fraction of the gemmae present is released during a time unit (see Fig. 2). In the model, we specifically assumed that production was zero on 1 May (the time when snow cover disappears) and on 15 October (just before appearance of new snow). This idea can be expressed as a differential equation $dN(t)/dt = at(5.5 - t) - cN(t)$, where N is the number of gemmae present, t is time in months starting from 1 May, a is a parameter that scales the maximum rate of gemma production, and $c > 0$ is the release rate of gemmae. This equation was integrated, and the resulting equation was fitted to the data in Table 1 using non-linear regression. Although the parameter estimates $a = 336$ (S.E. 216) and $c = 0.844$ (0.582) were not significantly different from zero, the model fits well the observed pattern of presence of gemmae, and the predicted rates are biologically reasonable (Fig. 2). The resulting model was used to calculate monthly estimates of gemmae released (Table 2).

Simulation results

Dormancy arose very rapidly in the model, especially during the latter part of the growing season (Fig. 4). After ca 500 yr, the germination schedule had reached a stochastic equilibrium: there were some fluctuations
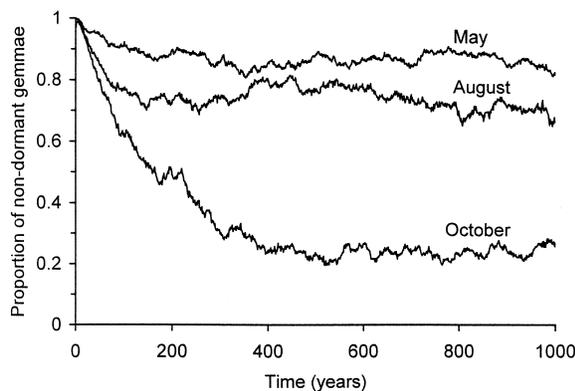

Fig. 4. An example of the evolution of the germination schedule in the individual-based model. In the beginning of the simulation, there is a strong directional selection towards production of higher numbers of dormant gemmae, especially late in the growth season. For clarity, only the trajectories for germinability in May, August and October are shown.
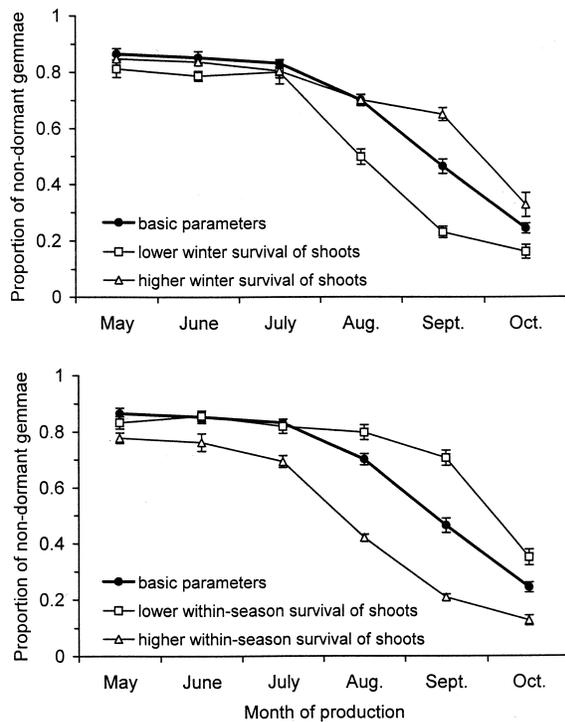
Fig. 5. Evolved germination schedule in the basic model (thick line) and when survival probabilities of shoots are varied (thin lines). In all cases, dormant gemmae become more frequent towards the end of growth season. Parameter values: basic, lower and higher winter survival, $s_{sw} = 0.90$, $s_{sw} = 0.75$ and $s_{sw} = 0.95$, respectively; basic, lower and higher within-season survival, $s_{ss} = 0.96$, $s_{ss} = 0.90$ and $s_{ss} = 0.99$, respectively.

in the population means of the proportion of non-dormant gemmae, but no long-term trends are apparent.

In the model selection favours the germination schedule with increasing tendency of dormancy towards the end of the growing season: the germinability was uniformly high during the first months, but then declined strongly (thick line in Fig. 5). Thus, the result of our model is in qualitative agreement with the field observations (Fig. 2), although the predicted germinability was somewhat higher than that observed during most of the season.

Figure 5 also illustrates the sensitivity of the predictions to changes in some parameter values. We see that germinability late in the season is influenced by survival of shoots during the growing season and in winter. If survival in winter is decreased, or survival during the growing season increased, the fraction of dormant gemmae produced increases, especially at the end of season. Conversely, when winter mortality is less severe, or mortality during the growing season higher, the frequency of dormancy decreases (Fig. 5).

The survival of dormant gemmae during winter only has a small effect on the model-predicted germination schedule, although slightly more dormant gemmae were

produced when their survival was higher (Fig. 6). The germination schedule was also insensitive to changes in within-season survival, where both types of gemmae had the same survival probability (Fig. 6). When only the survival of dormant gemmae was increased, the overall number of dormant gemmae produced remained similar, but on average, they were produced slightly earlier in the season.

Discussion

Germinability of gemmae of *Lophozia silvicola* shows a strong seasonal decline. We hypothesise that this decline is the consequence of an increasing frequency of dormant gemmae being produced. Our hypothesis is supported by the results of the simulation model developed for *L. silvicola*: there is a clear pattern of increasing frequency of dormancy towards the end of the growing season. Even though changes in parameter values cause changes in quantitative predictions, the overall seasonal pattern is remarkably robust. This also indicates that the gross ecological processes are captured well by the model.
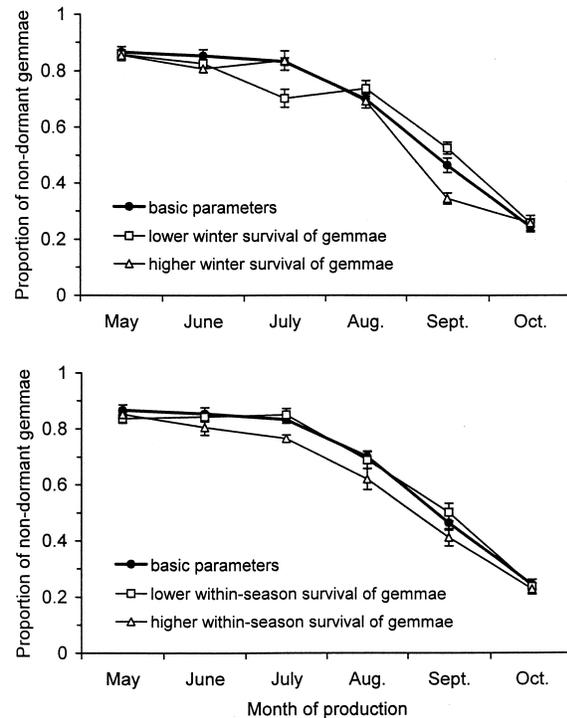

Fig. 6. The evolved germination schedules when survival probabilities of gemmae are varied. Parameter values: basic, lower and higher winter survival, $s_{dw} = 0.52$, $s_{dw} = 0.25$ and $s_{dw} = 0.75$, respectively; basic, lower and higher within-season survival, $s_{ds} = s_{ns} = 0.70$, $s_{ds} = s_{ns} = 0.60$ and $s_{ds} = s_{ns} = 0.80$, respectively.

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Direct evidence for existence of dormant gemmae in *L. silvicola* is still lacking. For example, we have no evidence that the gemmae that do not germinate in the liquid culture would do so after winter, nor that the gemmae that do germinate would have died during winter. However, presence of *L. silvicola* in the diaspore bank in boreal forest soil has been demonstrated previously by Jonsson (1993), although it is unknown whether the diaspores were gemmae or spores. Dormant gemmae are known in other hepatics: in the thalloid hepatic *Blasia pusilla*, two morphs of gemmae with differentiated roles have been reported (Duckett and Renzaglia 1993): stellate gemmae germinate instantly, but ellipsoid gemmae germinate only after overwintering. In *Lophozia silvicola*, no morphological differences can be observed between germinating and non-germinating gemmae. Thus, our results emphasize the need for further experimental studies on dormancy in *L. silvicola* gemmae.

The model predicts the observed pattern of germinability well, but there is a quantitative discrepancy: for most of the season, the predicted germinability is too high. One reason might be that the estimated survival of shoots during the growing season is too low (cf. Fig. 5). Current estimation of within-season survival assumes that a dead shoot will disappear in a month. If decomposition of dead shoots takes longer, then our survival estimates are too low. This is not unlikely as decomposition rate is affected by varying humidity.

Time-dependent dormancy (or diapause) has also been modelled in a number of earlier papers. Some models assume a sudden switch, from all diaspores germinating immediately, to all diaspores entering dormancy (e.g. Taylor 1980), whereas more flexible models allow gradual seasonal responses (Cohen 1970, McNamara 1994). In these models, gradual increase in dormancy requires environmental stochasticity in some form, either unpredictable season length or stochastic demographic rates. Thus, the results from our stochastic individual-based model agree with the earlier work.

Field data on the population ecology and life history of *Lophozia silvicola* are difficult to obtain. Thus, in addition to uncertainty in parameter values, some assumptions in the model structure are very tentative – they are based on observations rather than on quantitative measurements. These assumptions include the age at which shoots start to produce gemmae. The new shoots develop from germinated gemmae relatively slowly. In liquid culture, the germination of gemmae takes about three weeks. A shoot bud develops on the short protonemal tube emerging from a germinated gemma (Knoop 1984, Laaka-Lindberg 1999), but the differentiation of a new shoot occurs slowly. Juvenile shoots start to appear in the colonies during the first half of the growing season, but these do not carry gemmae until they reach a certain size

(Buch 1911). Thus two months was taken as a feasible estimate of the age at which the first gemmae are produced.

In general, *Lophozia silvicola* shoots are perennial, and capable of nearly indeterminate growth by branching. However, individual shoots with segments, indicating that growth occurred during more than three growing seasons, are rare. Shoot mortality is related to environmental conditions. The frequency of dead shoots was highest in May, after winter mortality has taken place (Table 2). The mortality rate, as judged from the number of dead shoots present, appears to be low during the growing season. However, roughly two-thirds of the yearly mortality takes place during the growing season (assuming decomposition time of one month for the dead shoots, see above). Variation in mortality is very high especially because of between-year and between-month variation in humidity.

Shoot density does not vary significantly between sampling months or between years (Table 1), indicating fairly stable dynamics at the population level, at least within the period under consideration here. The relative stability of shoot density indicates that repeated sampling itself does not affect the shoot density in the colonies.

The role of dormant asexually produced diaspores in turnover of *Lophozia silvicola* populations supports the view of asexual reproduction being an important means of maintaining local populations. In the study site in southern Finland, colonies of *L. silvicola* are covered by snow for half of the year. Mortality occurs also during the winter, but no colonisation can take place and vacant sites accumulate. Winter mortality is then compensated for by renewal of the colonies from dormant diaspores which readily germinate in the spring. During the growing season variation, especially in humidity, causes variation in mortality. In summer, dead shoots are replaced by new individuals germinating from available non-dormant diaspores. High between-year variation in monthly numbers of gemmae present on *L. silvicola* shoots is probably a consequence of varying weather conditions. This can be interpreted as an indication that environmental variability causes selective pressure in favour of the production of dormant gemmae (see Rees 1996, Hyatt and Evans 1998).

On the basis of our simulations, the amount of free space created by winter mortality relative to the free space becoming available during the growing season is expected to have a high impact on frequency of dormancy in a population. If mortality during the winter increases, then an increase in the proportion of dormant gemmae produced is favoured, while if within-season mortality is increased, the opposite will be true. These predictions could be tested by comparing populations living in different environments.

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