

## Population development, demographic structure, and life cycle aspects of two hornworts in Switzerland

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Population development and structure of the regionally annual hornworts *Anthoceros agrestis* and *Phaeoceros carolinianus* were studied in cultivated fields in the lowland of NW Switzerland. Ontogenetic stages of gametophytes and sporophytes were repeatedly surveyed at short time intervals in plots excluded from routine management during one growing season, and recruitment of *A. agrestis* was recorded in the subsequent season. *A. agrestis* was more abundant than *P. carolinianus* at the site scale, and its population development appeared to be more dynamic. The results suggest that in *A. agrestis*, gametophyte mortality is density-dependent in the early phase of its population development, and a minimum size for sexual reproduction occurs. Gametophyte recruitment probability from spores for *A. agrestis* was estimated at  $4.8 \times 10^{-5}$ . Mean gametophyte growth rate was 0.1 mm/d for both species. *P. carolinianus* gametophytes lived longer and grew larger than those of *A. agrestis*. Gametangial initiation, fertilisation, sporophyte development, and spore maturation occurred within a few weeks after germination in both taxa. Spore maturation peaked in August but sporophytes developed during the entire growing season in many plants.

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The population ecology and demography of bryophytes have received by far less attention than of vascular plants, and features of bryophyte life cycles are not commonly studied. Despite a number of elaborate demographic studies on bryophytes in the early development of plant population biology (Collins 1976, Hancock and Brassard 1974, Watson 1975, 1979), progress in this field for bryophytes has been slow (Økland 1995, 1997, 2000). Many processes important for population regulation are not yet well understood, and the scarcity of field data on various parameters of the species' biology has been quoted repeatedly (During and van Tooren 1987, Herben and Söderström 1992, Herben 1994, Söderström and Herben

1997). The lack of detailed basic knowledge of the biology of bryophytes also impedes any rational development of conservation actions for taxa that are negatively affected under their current environmental conditions.

Vital rates of birth, growth, and mortality describe the development of individuals through the life cycle, and their analysis is a necessary starting point for the study of population dynamics and life histories (Meyer and Schmid 1991, Silvertown and Lovett Doust 1993). Since individuals usually do not perform identically, and vital rates are age- or stage-specific, the population structure needs to be considered when assessing vital rates (Caswell 1989).

The two hornworts (Anthocerotopsida) occurring in Switzerland, *Anthoceros agrestis* Paton and *Phaeoceros carolinianus* (Michx.) Prosk., both monoicous taxa, are widespread in temperate regions of the world (Schuster 1992). They are usually annual in central

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and northern Europe as they do not survive the winter. In Switzerland they mainly grow in cultivated (commonly cereal) fields (Bisang 1992). Hornworts, in particular *P. carolinianus*, appear to be negatively affected by modern cropland farming practices in many European countries (Bisang 1997, 1998, 1999). During the past decades, research on the Anthocerotopsida has concentrated on developmental, ultrastructural, molecular and biochemical aspects, and the understanding of their systematics and phylogenetic affinities has considerably advanced (Mishler et al. 1994, Hedderson et al. 1996, Kenrick and Crane 1997, and references in Bisang 1995a). Characteristics of the population biology of hornworts, however, have hardly been considered until recently.

The present study is part of more extensive investigations on the population ecology of *A. agrestis* and *P. carolinianus*, aimed at increasing an understanding of their life cycles and the maintenance and regulation of their populations. In previous articles, I have outlined the distribution and threat status of the taxa in Switzerland, analysed the diaspore bank and its implications for population persistence, and examined the effects of management, weather and soil conditions on their occurrence (Bisang 1992, 1995b, 1996, 1998, 1999). The objectives of the present study are i) to describe the structure and development of an annual population through the growing season at the site scale for both taxa, and to compare them, and ii) to provide quantitative estimates of the life cycle parameters for growth, mortality and, for *A. agrestis*, recruitment.

## Methods

### Study area and study sites

The study was carried out in two arable fields in the lowlands of northwestern Switzerland, called the Swiss Central Plateau ('Mittelland'). The sites are situated at a distance of ca 5 km from each other in Bern, Enge-Viererfeld, at 560 m elevation, and in Muri, Bodenacker, at 530 m, both 46°55' N, 7°25' E (coordinates as to Landeskarte der Schweiz: 600.1/201.4 and 602.4/197.5). In these fields, one or both study species were known to regularly develop gametophytic populations, and habitat information and diaspore bank data were available from previous investigations (Bisang 1996, 1998). The climate in the area is humid-temperate with a mean temperature of -1.5 °C in January, 17 °C in July, and an annual precipitation of 100 cm. The soils of the study fields are subneutral, weakly humose and are classified as sandy loams (Bisang 1998: fields No. 27 and 28). Crop-rotation is the traditional and conventionally applied land use prac-

tice in the Swiss Central Plateau, alternating between bread cereals (most commonly wheat), maize, artificial fodder meadows, potatoes and rarely other root-crops, and occasionally pastures. In contrast to the first half of the last century, the harvests today take place earlier in the season (second half of July / early August), and are immediately or very soon succeeded by tillage operations.

In field I, wheat was grown during the study years. The regionally prevalent practice is autumn tillage, but in autumn 1992 this field was not processed. Instead, it was ploughed and cultivated with a spring-sown wheat variety in spring 1993. *A. agrestis* was found in its eastern end which was shaded during part of the day by trees of an avenue. Due to an agreement with the farmer in charge to exclude an area of ca 100 m<sup>2</sup> of the field from ordinary cultivation, *A. agrestis* could be studied without the immediate influence of arable farming manipulations during the growing season. The second field was used as a hay meadow. Both *A. agrestis* and *P. carolinianus* occurred there, mainly along the southwestern margin bordering a riverine wood. The first known collection of the latter species at this locality dates back to 1880 (Bisang 1997). A similar arrangement as for field I could not be obtained with the landowner of this site, and other fields with *P. carolinianus*, which is much rarer in Switzerland (Bisang 1992, 1998), were not available in the neighborhood. However, the SW border was very unproductive due to its proximity to the forest, and was therefore basically left unmanaged during the main season.

### Field surveys and data collection

From May 1992 onward the fields were inspected regularly at the beginning of every month to check for germination of hornworts. In July, about one week after emergence of hornwort sporelings, three study plots, which well represented the developing population of *A. agrestis*, were placed in the section of field I that was excluded from routine management. In field II, three plots were set up along the southwestern margin including as many individuals as possible of *P. carolinianus* (n = 5). Metal bars fixed in the soil served as plot markers and to adjust a frame with a one-centimeter grid used for the population inventories. Plot size was 30×30 cm<sup>2</sup>, except for one plot in field I which was half as large due to practical restrictions. Gametophyte and sporophyte numbers (see following) in the latter plot were extrapolated to standard plot size. All gametophytes and sporophytes in each plot were counted, first at weekly intervals, then every 13 to 18 days, and finally after three weeks on 30 November. The plots in field II were not surveyed

on the last occasion after having been affected by a tillage operation that involved also the SW field margin in the middle of November. Gametophytes were classified into four size classes, to account for ontogenetic stage: < 3 mm in diameter (juvenile), 3–10 mm (small), 11–20 mm (intermediate), and > 20 mm (large). Sporophytes were assigned to one of three developmental states: immature and green; mature, but unopened; and post-mature and dehisced. Spores of *Anthoceros* turn dark brown at maturity, and yellow in *Phaeoceros*, and accordingly, the capsule walls change colour. All *P. carolinianus* plants, and five *A. agrestis* individuals chosen at random in each plot, were mapped to grid co-ordinates, and their gametophyte diameter and sporophyte number monitored during the season. Also, the length of the green and mature portions of one randomly selected and marked capsule per surveyed thallus was measured at each census. Many *A. agrestis* gametophytes died during the growing season. These were replaced by other individuals that were mapped and surveyed (these are not displayed in Fig. 2A) resulting in a sub-set of  $n = 27$  individually followed plants of which three gradually degenerated during the observation period. Daily growth rates were calculated by dividing diameter increase by life length in number of days (for the  $n = 24$  expanding thalli). Data from the last census (30 November) were excluded from these calculations as many plants had started to deteriorate.

In 1993, study plots were established in field I as described above for the preceding year, and the survey initiated in the beginning of August. No plots were set up in field II since *P. carolinianus* did not develop gametophytes in summer 1993. The monitoring of *A. agrestis* in field I was abruptly terminated by the harvest of the field in early August 1993 which inadvertently included the study section. The hornwort gametophytes did not survive the cropping, thus the study interval is restricted basically to one season. Nevertheless, the first census performed in 1993 allowed an approximation of recruitment probability under field conditions for *A. agrestis*: assuming a comparable population development as in 1992, the total number of potentially emerging gametophytes in 1993 was estimated based on the number of thalli recorded in the course of the population inventory on 2 August 1993 and the maximum time since germination, i.e. the previous check when no sporelings were observed (13 July). This number was related to the production at the same site in 1992. The spore production estimate takes into account the numbers of mature, unopened and postmature, dehisced capsules assessed in this survey, a mean length for these calculated on the basis of the measurements on the individually marked sporophytes, and the spore content per unit length of mature sporangia (see Bisang 2001 for details).

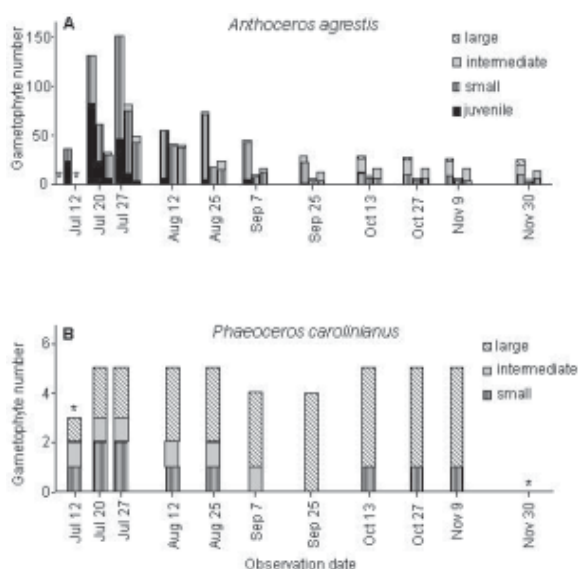


Fig. 1. Structure of gametophyte populations of *Anthoceros agrestis* (A) and *Phaeoceros carolinianus* (B) in three study plots (totally 2700 cm<sup>2</sup>) in cultivated fields in Switzerland during one growing season, differentiated as to size classes. *Phaeoceros* plants from the three plots are pooled because of low numbers. Gametophyte diameter: juvenile, < 3 mm; small, 3–10 mm; intermediate, 11–20 mm; large, > 20 mm. \*, plot(s) not surveyed, thus, the first column in 1B represents only two plots and is not directly comparable with the others. Bars in 1A representing observations on 12 and 27 July are slightly laterally displaced to fit into the graph. Note the different scales on the y-axes in A and B.

Nomenclature, unless otherwise stated, follows Corely et al. (1981) and Corley and Crundwell (1991) for mosses, and Grolle (1983) for hepatics. Despite the growing evidence that ‘bryophytes’ are not monophyletic (Mishler et al. 1994, Hedderson et al. 1996, Kenrick and Crane 1997), I will refer to bryophytes including the Anthocerotopsida as a grade of green plants that share a similar life cycle and a number of similar character states.

## Results

### Development and structure of gametophytic populations

Sporelings of *Anthoceros agrestis* were encountered in 1992 at both study sites in early July. At this time, they had reached a diameter of 1 to 3 mm. The majority of spores germinated in July within a month, but some germination occurred in one plot until September (Fig. 1A). In 1993, sporelings were again observed in early July in field II, but only in the beginning of August in field I. The density of juveniles and small

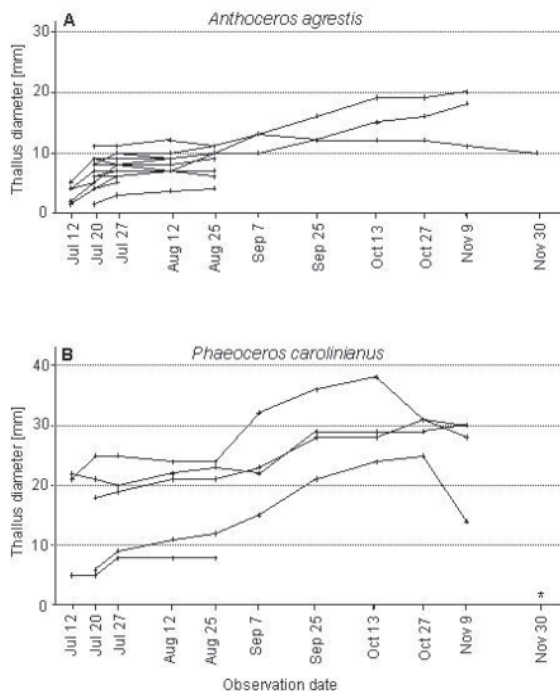


Fig. 2. Thallus diameter of individually followed plants of *Anthoceros agrestis* (A; n = 15) and *Phaeoceros carolinianus* (B; n = 5) in cultivated fields in Switzerland during one growing season. Only plants monitored from the beginning of the survey (starting either on 12 or 20 July) are included.

gametophytes was quite high, up to 150 gametophytes per 900 cm<sup>2</sup> were counted in 1992 (Fig. 1A). Gametophyte number peaked towards the end of July in all plots. A distinct decline of gametophytes occurred between the recording dates 27 July and 12 August. The loss was most pronounced in the plot shown to the left in Fig. 1A. In this, no plants grew larger than 1 cm until the end of August. Gametophyte mortality in individual plots during this time interval was 64%, 49%, and 17%, respectively, in relation to the gametophyte number present at the beginning of this period (27 July; plots from left to right). Apparently, mortality increased with gametophyte density in this early phase of population development. Distinct growth was further observed in the end of September and early October when a number of individuals expanded to more than 1 cm in diameter ('intermediate'). The maximum size, however, was limited: only three plants in one of the plots reached a diameter of more than 2 cm ('large').

Sporelings of *Phaeoceros carolinianus* were also observed in early July in 1992, but were much fewer than those of *A. agrestis* (Fig. 1B). All thalli had grown larger than 3 mm at this time (Fig. 2). Gametophyte density over the entire field II appeared to be even lower. In a search of the whole field in September 1992,

eleven individuals with a diameter of > 2 cm were counted within a field portion of ca 40 m<sup>2</sup>. All studied plants attained more than 2 cm in diameter until the end of September. One of five surveyed individuals died, and no germination occurred later in the autumn. The apparent emergence of a small gametophyte in October (Oct 13, Fig. 1B) originated from fragmentation of a larger one.

The mean diameter increase was similar for both taxa at 0.1 mm/day (*A. agrestis*: mean = 0.11, sd = 0.07 mm, n = 24 selected repeatedly measured gametophytes; *P. carolinianus*: mean = 0.10, sd = 0.06 mm, n = 5). *A. agrestis* individuals had generally a shorter life-span and grew smaller than *P. carolinianus* plants (Fig. 2). If we approximate life span to one and a half months, the mean growth rate of 0.1 mm/d corresponds to a radial thallus expansion of 2.3 mm. The initial average diameter of *A. agrestis* gametophytes recorded at the beginning of the survey was 5.5 mm (sd = 2.8, n = 15). Accordingly, the total seasonal thallus expansion amounts to 10.0 mm (sd = 2.8) or ca 0.8 cm<sup>2</sup> in terms of surface area, presuming circular thalli. For individuals that survive a large part of the growing season (approximately three months), seasonal thallus expansion is 14.5 mm (sd = 2.8) and surface increase ca 1.8 cm<sup>2</sup>. The corresponding figures for *P. carolinianus* with an initial mean diameter of 14.4 mm (sd = 8.3, n = 5) and a presumed life span of three months are 23.4 mm (sd = 8.3) and 4.3 cm<sup>2</sup>.

#### Recruitment rate of *Anthoceros agrestis*

Since the study plots were inadvertently involved in the harvest of the field in 1993 only one census was conducted in the beginning of August. This was at most 19 days after hornwort emergence as no signs of germination had been observed at the previous inspection on 13 July. In four plots of 30×30 cm<sup>2</sup>, I recorded an average of 36 gametophytes per plot. In 1992, about 60% of the total gametophytes had appeared 19 days after the germination onset. I thus estimated that about 60 gametophytes per plot, or 180 in the area equivalent to that surveyed in 1992 (three plots of 2700 cm<sup>2</sup> in total), would emerge in 1993. Mature spore production was estimated to 3,747,380 in the survey area of 2700 cm<sup>2</sup> (Bisang 2001). Accordingly, gametophyte recruitment probability from spores was assessed as 4.8×10<sup>-5</sup>.

#### Sporophyte development

In *A. agrestis*, 95% of the individually followed gametophytes produced sporophytes. Sporophytes usually appeared three to four weeks after germination on plants that had reached at least 3 mm in diameter (Fig.

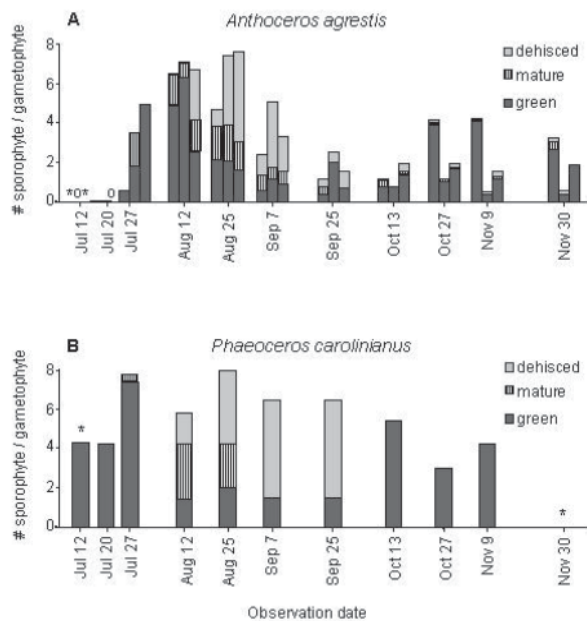


Fig. 3. Mean number of sporophytes per gametophyte during one growing season in *Anthoceros agrestis* (A) and *Phaeoceros carolinianus* (B) in three study plots (totally 2700 cm<sup>2</sup>) in cultivated fields in Switzerland, differentiated as to maturity states: immature and green; mature, but unopened; and post-mature and dehisced. \*, plot(s) not surveyed, thus, the first column in 3B represents only two plots and is not directly comparable with the others. Bars in 3A representing observations on 12 and 27 July are slightly laterally displaced to fit into the graph.

3A). No capsules were observed on monitored individuals smaller than 3 mm. The first spores reached maturity within about one month after germination. Sporophytes were usually visible and had probably continued to grow and thus to produce mature spores for about one to two weeks after the gametophytes had started to decay. This explains the temporal divergence between the peaks in gametophyte density and sporophyte number (Fig. 1A vs 3A). Sporangia number was highest in August in all plots, in terms of both absolute numbers (up to 350 capsules per colony area of 900 m<sup>2</sup>) and the mean per gametophyte (Fig. 3A). The largest proportion of spore-shedding capsules was observed at the end of August. New sporophytes appeared again in two plots later in the season, reaching a second peak in one plot. Limited spore maturation continued until the end of November. Mean sporophyte number per thallus over the entire season was 3.4, 4.1 or 6.0 in individual study plots. Mean sporophyte number did not significantly differ between gametophytes with a diameter 3 to 10 mm ('small') and gametophytes from 10 to 20 mm ('intermediate') (Mann-Whitney test,  $p = 0.87$ ;  $n = 27$  individually followed plants).

All study plants of *P. carolinianus* formed sporophytes which emerged earlier than those of *A. agrestis* (Fig. 3B). As in the latter, sporophytes developed also from mid October until mid November. However, no spore maturation occurred later than the end of September. Mean sporophyte number per gametophyte over the entire season was 4.5, 8, or 23 in individual study plots.

## Discussion

The population structure and dynamics have been analysed in detail in relatively few bryophyte species to date despite recent progress in the field (Corradini and Clément 1999, Hobbs and Pritchard 1987, Lloret 1991, Økland 1995, 1997). To my knowledge, the present study is the first dealing with the demographic structure and development of hornworts populations, and one of rather few that considers life cycle aspects in an ephemeral bryophyte occurring in a transient habitat (McLetchie 1992, 1999, Pettet 1967). Unfortunately, its small scale (one season; one field for each taxon, thus lack of true replicates; few surveyed *P. carolinianus* individuals) limits the possibility to generalise the recognised patterns, and restricts the discussion to the studied populations. However, the present data are substantiated by results from a repeated survey of 28 populations of *Anthoceros agrestis* and *Phaeoceros carolinianus* in the study area during seven years (Bisang 1998). Thus, they provide insight into the basic trends in the population development of these taxa and information on processes important for population regulation. They hopefully will stimulate further work in a field that is poorly understood and suffers from scarcity of field data (Söderström and Herben 1997).

### Recruitment, development and structure of gametophytic populations

Both taxa are apparently able to germinate in cereal fields before cropping though some germination also occurs later in the season in *A. agrestis* (Fig. 1). Observations on many hornwort populations from 1984 to 1996 corroborate this finding (Bisang 1998 and unpubl. data) even though literature reports on hornwort establishment in fields before harvest are lacking so far. In field I, emergence of *A. agrestis* was about one month later in 1993 than in 1992. This might be a consequence of different farming practices, i.e. spring tillage in 1993 compared to autumn ploughing in 1991, or due to between-year differences in weather conditions. In field II which was used as a hay meadow in

both years, *A. agrestis* sporelings were about as abundant in mid-July in 1993 as in 1992. Therefore, I favour the former interpretation.

During the early phase of population development, mortality rate of *A. agrestis* appeared to be positively related to gametophyte density at the end of July. In the two plots shown to the right in Fig. 1A, with lower densities than the left plot, no more gametophytic remains were observed than expected from the decline in gametophyte number (pers. obs.), and no juveniles were found on 12 August. This suggests that the recorded mortality is not obscured by delayed germination and immediate death of sporelings in the two right plots between the censuses on 27 July and 12 August. Both positive and negative effects of density on shoot survival and performance have been reported in bryophytes to date. While beneficial density effects may arise through improved microclimatic conditions for growth within intact bryophyte colonies, negative density dependence may be caused by increased competition for resources, presumably light (overview in Pederson et al. 2001). For thalloid bryophytes, space may be a primary resource for gametophyte growth and development, especially if germination is clumped as in the study taxa, and increased density can thus negatively affect the survival of the individuals. Gametophyte extinction during the growing season was also induced by temporarily or locally occurring drought, and small-scale destruction of the soil surface by precipitation or the activity of small mammals (pers. obs.; 'catastrophic deaths', Collins 1976). Further observations suggest that predation may affect hornworts (slugs, pers. obs.; crane fly larvae, Bisang et al. 1996) and that *A. agrestis* gametophytes are competitively inferior as they are overgrown by pleurocarpous mosses, moss protonemata, or algae.

The number of individuals in the *P. carolinianus* population appeared rather constant but was markedly lower than in *A. agrestis*. This agrees with the results from the seven-year monitoring of 28 hornwort populations, where *P. carolinianus* was encountered in 0–4 fields per year, and formed only once a copious population with plenty of sporophytes (Bisang 1998). The taxon is thus rare both at the site scale and at the regional scale in Switzerland.

Growth in bryophytes is highly species-specific (Russell 1984) and known to be related to water supply and hence to macro-climatic and micro-scale moisture conditions (Vitt 1991, Bates 1993, Hanslin 1999). Yet, the mean growth rate over the entire season is similar for both study taxa. *P. carolinianus* thalli are generally longer-lived than those of *A. agrestis* and thus attain larger sizes (Fig. 1 and 2). Data for other species of the annual shuttle strategy (sensu During 1979, 1992) and/or with a thalloid growth form under field conditions are scarce. Bates (1993) reported mean

annual lobe elongations of 8.7 and 24.7 mm for *Pallavicinia lyellii* and *Pellia epiphylla*, respectively, on streambanks in southern England. They are comparable with the seasonal thallus expansion values obtained for Swiss hornworts (10–23.4 mm). Growth rate of mature thalli of the tropical *Riccia nigrosquamata* E.W. Jones amounts to 1 mm per week (Berrie 1975) or ca 0.16 mm/day which is in the order of magnitude of the study species. Finke (1998) measured a maximal thallus area extension of 6 mm<sup>2</sup>/day for the annual *Riccia glauca* on arable fields in central Germany, restricting the measurements to the most productive phase in its life span. However, the photographic method employed does not allow a direct comparison with the present data.

At the first census in July, all *P. carolinianus* plants had already reached more than 3 mm in diameter, and thus grown larger than most individuals of *A. agrestis*. It remains to be shown if this was due to faster growth in the juvenile stage or due to a greater age of *P. carolinianus* at that time. They could have emerged up to one month before *A. agrestis* since the fields were searched for sporelings once a month before the start of the censuses.

A potential source of error for the estimate of the recruitment rate for *A. agrestis* may be the fact that the population development could not be fully surveyed in 1993. Thus, the present value indicates the order of magnitude of the establishment probability for *A. agrestis* under relatively undisturbed conditions (i.e. excluded from arable management). Recruitment from spores under field conditions has been studied for only a handful of bryophytes so far, not including shuttle species. Either no field germination, or establishment rates between  $9 \times 10^{-4}$  and  $5 \times 10^{-3}$  were reported (Miles and Longton 1990, Hassel and Söderström 1999).

### Sporophyte development

Gametangial initiation, fertilisation, and sporophyte development to maturation took place within a few weeks after germination both in *A. agrestis* and *P. carolinianus*. This supports predictions from life history theory for short-lived bryophytes (low age for first reproduction; During 1979, Longton 1997). Reproductive maturity within a few weeks or months after gametophyte establishment was likewise reported for the annual taxa *Riccia nigrosquamata* (Berrie 1975) and *Physcomitrella patens* subsp. *californica* (Crum and Anderson) Tan (Une and Tateishi 1996).

In *A. agrestis*, no sporophytes were observed on juvenile gametophytes smaller than 3 mm. This suggests that a minimum size (resource level) for sexual reproduction occurs. A well-defined minimum shoot

size for sporophyte production was identified in *Hylocomium splendens* (Rydgren et al. 1998) while Convey and Lewis Smith (1993) did not find a distinct reproductive size threshold in a number of Antarctic mosses.

### A comparison of life cycle traits in *A. agrestis* and *P. carolinianus*

In Central Europe, generations of *A. agrestis* and *P. carolinianus* usually last less than one year and hence do not overlap. Both taxa classify as annual shuttle species in the life strategy system proposed by During (1979, 1992). Growth, reproduction and death are not restricted to discrete times but occur more or less continuously during the growing season and within the population, except that juveniles do not reproduce sexually. Annual life cycles exhibiting continuous growth and reproduction until terminated by a climatic event are commonly represented among flowering plants, and are placed in the "opportunistic" life cycle category (Harper 1977). Despite the general similarity of the life histories of *A. agrestis* and *P. carolinianus*, their population dynamics in cultivated fields in the Swiss Central Plateau differ in some aspects. Populations of *A. agrestis* are highly dynamic and opportunistic in that numerous gametophytes and sporophytes are produced within a short time, and that gametophytic growth and spore maturation potentially extend over long periods of the growing season and over nearly the entire gametophytic life span. The population size of *P. carolinianus* is smaller and the structure comparatively more stable. Mortality is lower, sporophytes tend to be shorter, and both germination and spore maturation are restricted to shorter periods than in *A. agrestis*. Thus, the timing of germination and spore maturation and other features of the population development appear less plastic in *P. carolinianus* than in *A. agrestis*. This might be one reason why the former has declined more strongly than the latter under the changing conditions in the agro-ecosystems of Central Europe (Bisang 1992, 1998, 1999). However, the degree to which these differences are biologically based, or are an effect of the agricultural management history, cannot be judged with the present information. The short life-span of the two species in Central Europe is apparently climatically conditioned. A prolonged gametophyte growth under favourable environmental conditions has been described for these and other hornwort taxa (Bisang 1995a). Of the two study species, *P. carolinianus* survives longer than *A. agrestis* in culture (e"18 vs 11 months; Bisang 1995a) and only the former is reported as a facultative perennial from some regions (Schuster 1992: southern Appalachians) which is in accordance with the tendency

towards stability of its populations and individuals observed in this study.

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