

The relative importance of sexual and clonal reproduction for population growth in the perennial herb *Fragaria vesca*

Juerg Schulze · Rita Rufener · Andreas Erhardt · Peter Stoll

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Abstract The relative importance of sexual and clonal reproduction for population growth in clonal plants is highly variable. Clonal reproduction is often more important than sexual reproduction but there is considerable interspecific variation and the importance of the two reproductive modes can change with environmental conditions. We carried out a demographic study on the woodland strawberry (*Fragaria vesca*), a widespread clonal herb, at 12 sites in Switzerland during 2 years. Study sites were selected in two different habitats, i.e., forest and forest edge. We used periodic matrix models to estimate annual population growth rates and carried out prospective analyses to identify life cycle components that influence population growth rates most. Retrospective analyses were applied to study how the two different habitats affected population dynamics. Furthermore, we tested whether trade-offs between sexual and clonal reproduction occurred. There were large differences in annual population growth rates between sites and large within-site differences between years. Results of the prospective analyses clearly indicate that clonal reproduction is the dominant reproductive pathway whereas sexual reproduction is rather insignificant for population growth. Compared to forest habitats, forest edge habitats had higher population growth rates in the first year but smaller growth rates in the second year. We attribute these differing habitat effects to different

water availabilities during consecutive years. No trade-offs between sexual and clonal reproduction were found. In conclusion, population growth of *F. vesca* relies heavily on clonal reproduction. Furthermore, reproduction and survival rates of *F. vesca* depend highly on spatio-temporal variation of environmental conditions.

Keywords Clonal plants · Demography · Life table response experiment · Matrix population model · Trade-off

Introduction

The relative importance of sexual and clonal reproduction for population growth and maintenance in clonal plants has been studied in a variety of species differing in life history and habitat requirements (e.g., Damman and Cain 1998; Mandujano et al. 2001; Wepler et al. 2006; Alfonso-Corrado et al. 2007; Schleuning et al. 2008). Many clonal plant species rarely recruit by seeds (Eriksson 1997) but there can be considerable variation among species (Eriksson 1992, 1997; Silvertown et al. 1993). In clonal plants, clonal reproduction is often more important for population growth than sexual reproduction (Alfonso-Corrado et al. 2007; Schleuning et al. 2008) although the two reproductive modes seem to be of rather equal importance in some species (Damman and Cain 1998; Wepler et al. 2006). However, it is not always easy to assess the relative importance of sexual and clonal reproduction for population growth as it can change under different environmental conditions (Mandujano et al. 2001).

The reasons for the maintenance of sexual reproduction in clonal plants and antagonisms between sexual and clonal reproduction are complex and not clearly resolved (Eriksson 1997; Silvertown 2008; Vallejo-Marin et al. 2010). On an

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J. Schulze (✉) · R. Rufener · A. Erhardt · P. Stoll
Section Conservation Biology (NLU),
Department of Environmental Sciences, University of Basel,
St. Johanns-Vorstadt 10, 4056 Basel, Switzerland
e-mail: juerg.schulze@stud.unibas.ch

evolutionary scale, advantages of sexual reproduction are the maintenance of genetic diversity and the generally larger dispersal capacity of sexually produced propagules which makes a species more flexible to respond to environmental variation and disturbances (Eriksson 1997; Silvertown 2008). However, when sexual and clonal reproduction occur simultaneously or consecutively in an organism, this can lead to allocation trade-offs between the two reproductive modes. Such trade-offs can be resource-based or be caused by a limited number of meristems that are available for either sexual or clonal reproduction (Vallejo-Marin et al. 2010). Trade-offs have been shown in studies of phenotypic correlations between reproductive modes (Sutherland and Vickery 1988; Snow and Whigham 1989; Geber et al. 1992; Worley and Harder 1996) and allocation patterns to sexual or clonal reproduction can vary within species under changing environmental conditions (Prati and Schmid 2000; Liu et al. 2009; Xiao et al. 2011). However, there are also studies that did not find trade-offs (Reekie 1991; Mendoza and Franco 1998; Thiele et al. 2009).

Matrix population models (Caswell 2001) are a powerful tool to assess the relative importance of plant vital rates, i.e., growth, survival, sexual and clonal reproduction, for population growth (e.g., Mandujano et al. 2001; Weppeler et al. 2006; Jongejans et al. 2008). To analyse the relative influence of different vital rates on the finite rate of population growth (λ), prospective and retrospective analyses of matrix population models can be used (Caswell 2001). Prospective analyses, such as elasticity analyses, explore how small changes in the vital rates would affect λ (de Kroon et al. 1986; Caswell 2001). Retrospective analysis approaches, such as life table response experiments (LTRE), quantify the contribution of the actual variability in the vital rates caused by an environmental factor to the resulting variability in λ (Caswell 2001).

We carried out a demographic study on the woodland strawberry (*Fragaria vesca* L.), a perennial stoloniferous herb and the most common species in the genus *Fragaria* (Rosaceae) (Hancock 1999). In Switzerland, *F. vesca* is common in sparse forests and at forest edges and occurs from the lowlands up to the subalpine zone (Binz and Heitz 1990). It is insect pollinated and reproduces clonally through formation of above-ground stolons (Hancock 1999). Its wide distribution and the ease with which clonal reproduction can be followed non-invasively makes it an ideal study species for population biology. To capture environmental heterogeneity, *F. vesca* populations were studied at 12 sites in northwestern Switzerland over 2 years. Moreover, plant populations were selected from two different habitat types, i.e., forest and forest edge habitat. The demographic data were used to parameterize periodic stage-structured matrix population models, and we applied elasticity analyses and LTREs (Caswell 2001).

We addressed the following main questions: (1) what is the relative importance of sexual and clonal reproduction for population growth in *F. vesca*? (2) How do different habitats affect vital rates and population dynamics? (3) Do trade-offs between sexual and clonal reproduction occur?

Methods

Study species

Fragaria vesca (Rosaceae) is the most widely distributed *Fragaria* species and occurs throughout the northern hemisphere (Hancock 1999). It is an erect rosette plant and 15–30 cm tall. Leaves carry an axillary bud which can develop either into an above-ground stolon, a branch crown or an inflorescence (Darrow 1966). Floral induction is controlled by temperature and photoperiod (Heide and Sønsteby 2007) and usually takes place in fall in the study region. The initiated flower buds continue their growth in the following spring and the bisexual and self-compatible flowers mainly flower from April to June in low altitudes (Binz and Heitz 1990). Plants reproduce clonally through formation of nodes that grow from stolons. Clonal reproduction usually takes place after flowering and stolons are produced from summer till fall (Angevine 1983; J. Schulze, personal observation). Nodes form adventitious root primordia that will root when in contact with moist substrate (Angevine 1983). Connected *F. vesca* ramets are physiologically integrated and young plants can receive resource supply from mother plants (Roiloa and Retuerto 2006, 2007). Depending on environmental conditions the stolon connections between ramets stay intact for weeks or several months but they are usually lost by spring (Angevine 1983; J. Schulze, personal observation).

Study sites and plots

In summer and fall 2007 and spring 2008, we went on excursions in northwestern Switzerland to look for study sites. The criteria for site selection were the presence of established *F. vesca* populations and the location at similar elevations within the collin zone. Furthermore, study sites had to be located in forest or forest edge habitats (Table 1). Within every population we marked a permanent rectangular plot with an area ranging from 0.69 to 4 m² depending on plant density. A grid of 0.25 × 0.25 m squares was established within plots, and corners of plots were marked with wooden pegs and a piece of metal in case a plot had to be recovered with a metal detector. At every census a cord was spanned along the outline of the plots and the inner grid subdivisions were determined with a measuring stick.

Table 1 Information on study sites, clonal and sexual reproduction and growth rates λ of natural *F. vesca* populations

	Adlerberg	Eichmatt	Gempen	Grammet	Schauenburg	Schleifenberg	Ziefen	Holzenberg	Hochwald	Paradies	Riehen	Scharten	All sites
Altitude (m a.s.l.)	450	600	720	520	480	440	520	650	630	430	490	730	–
Coordinates north/east	47°30'24"/7°42'12"	47°29'49"/7°39'10"	47°28'43"/7°39'33"	47°29'09"/7°46'02"	47°29'50"/7°41'02"	47°29'28"/7°44'10"	47°26'08"/7°42'22"	47°25'12"/7°41'04"	47°27'00"/7°37'27"	47°30'17"/7°41'53"	47°34'35"/7°40'49"	47°28'38"/7°39'09"	–
Plot area (m ²)	1.13	1.88	2.00	1.75	1.75	0.69	1.69	0.75	1.13	1.50	4.00	0.88	–
Site type	Forest	Forest	Forest	Forest	Forest	Forest	Forest	Forest edge	Forest edge	Forest edge	Forest edge	Forest edge	–
Mean clonal offspring 2008	0.27 ± 0.64	0.49 ± 0.91	1.89 ± 2.24	1.90 ± 2.12	3.00 ± 3.07	0.50 ± 0.92	0.66 ± 1.07	3.82 ± 2.26	8.13 ± 6.78	8.57 ± 6.30	0.23 ± 0.73	2.58 ± 2.33	2.47 ± 4.02
Mean clonal offspring 2009	0.11 ± 0.34	0.06 ± 0.35	0.44 ± 1.12	1.39 ± 2.24	3.86 ± 3.59	0.06 ± 0.25	0.21 ± 0.66	0.65 ± 1.28	1.16 ± 1.90	0.90 ± 1.47	0	0.80 ± 1.43	0.83 ± 1.90
Mean ripe fruits 2008	0.12 ± 0.47	0.48 ± 1.08	0.40 ± 1.09	0.26 ± 0.73	0.06 ± 0.29	0.08 ± 0.40	0.15 ± 0.54	1.52 ± 1.98	0.05 ± 0.28	1.25 ± 2.89	0.51 ± 0.89	0.78 ± 1.34	0.46 ± 1.28
Mean ripe fruits 2009	0.06 ± 0.31	0.30 ± 0.88	0.02 ± 0.14	0.55 ± 0.84	0.25 ± 0.90	0.11 ± 0.32	0.21 ± 0.58	1.12 ± 1.10	1.66 ± 1.81	2.16 ± 2.98	0.22 ± 0.50	1.27 ± 1.41	0.66 ± 1.41
Seedlings found 2008	1	2	0	0	0	0	0	0	1	0	2	0	6
Seedlings found 2009 ^a	2	0	0	0	0	0	0	3	0	0	0	0	5
λ 2008–2009	1.13	0.41	1.65	1.10	3.04	0.64	1.19	1.89	4.92	6.08	0.37	1.85	1.61
λ 2009–2010	0.64	0.09	0.46	0.25	2.34	0.03	0.43	0.40	0.37	0.17	0.04	0.35	0.28
Mean λ	0.85	0.25	1.06	0.68	2.74	0.33	0.81	1.14	2.68	3.14	0.21	1.11	0.94

Mean values are given with \pm SD

^a No new seedlings were found during the final census in spring 2010

In June 2008, the relative light transmission, i.e., the ratio of transmitted radiation to total radiation above the canopy, at study sites was calculated. Pictures of the canopy closure above the plots were taken with a fish eye objective lens and were analysed with the Gap Light Analyzer software (Frazer et al. 1999) with default values for all radiation parameters. Mean relative light transmission values were $27.4 \% \pm 7.9$ SD and 60.2 ± 22.5 SD at forest and forest edge habitats, respectively.

Precipitation data

We obtained monthly precipitation data from four weather stations from the Swiss Federal Office of Meteorology and Climatology. The weather stations were distributed in and around the study area, i.e., in Arisdorf ($47^{\circ}30'53''\text{N}$, $7^{\circ}46'45''\text{E}$), Binningen ($47^{\circ}32'28''\text{N}$, $7^{\circ}35'01''\text{E}$), Laufen ($47^{\circ}25'05''\text{N}$, $7^{\circ}29'52''\text{E}$) and Riehen ($47^{\circ}34'27''\text{N}$, $7^{\circ}37'26''\text{E}$). Monthly precipitation data of 2008 and 2009 were compared with paired two sample *t* tests. Mean annual precipitation was 958 mm (± 54 mm SE) in 2008 and 856 mm (± 53 mm SE) in 2009. In 2009, precipitation was significantly lower during periods that are important for growth and clonal reproduction of *F. vesca* plants, i.e., in April, August, September and October [S1 in Electronic Supplementary Material (ESM)].

Data collection

Data collection started in spring 2008 and either all or a selection of *F. vesca* plants present in the plots were marked with coloured wire below the oldest leaf. Initially, we marked between 66 and 101 plants per plot (total 947 plants) and mapped them on hand-drawn maps. If plants were numerous only a random selection of plants was marked, representing similar numbers of all the present plant sizes.

The first intra-annual census was carried out at the end of April and a second and a third census were conducted 4 weeks (end of May) and 8 weeks (end of June) later. The dates were chosen so as to cover the main flowering and fruiting period of *F. vesca*. A fourth intra-annual data collection was carried out in the middle of September to cover autumn stolon production. Data collection from marked plants included measurement of (1) length of middle leaflet of live leaves (i.e., ≥ 50 % of leaf area of green colour), (2) sexual reproduction, i.e., number of inflorescences, presence or absence of open flowers, number of developing and ripe fruits, number of fruits gone (empty calyx present) and (3) clonal reproduction, i.e., number of stolons and number of nodes. Seasonal censuses were completed within <15 days for all 12 sites, depending on weather conditions.

In April, June and September, plants were measured and sexual and clonal reproduction were recorded. In May, only sexual reproduction was recorded. At all censuses seedlings were searched for and all seedlings were marked with coloured wire and mapped. We could find only very few seedlings and therefore planted seedlings into plots to estimate survival rates of seedlings. Ripe fruits were collected at each study site, cut in half and air dried on blotting paper. Seeds were collected from dried fruits and germinated on soil collected from study sites in a greenhouse. In the middle of August, 40 seedlings with one or two leaves were transplanted to each plot. At each end of the plots, 20 seedlings were planted in two parallel rows separated by 20 cm and a distance of 1.5 cm between seedlings. Survival of seedlings was recorded at every subsequent census.

The lifetime of stolons is dependent on environmental conditions. Under unfavourable conditions connections between mother plant and nodes can die off within weeks, but they usually stay intact throughout the growing season and finally wither in fall or winter (Angevine 1983; J. Schulze, personal observation). Therefore, clonal reproduction of plants can be assessed rather accurately by two censuses in summer and fall. To estimate survival and growth of nodes, 20 newly formed nodes, or as many as could be found if there were less, were marked and mapped at each plot in June and September.

In spring 2009, we measured all plants present in plots to determine actual plant size structures.

Estimation of vegetative above-ground biomass

To estimate the vegetative above-ground biomass of plants non-destructively, we modeled the correlation of leaf lengths and dry weights of leaves. Inflorescences were not included in biomass estimation. Leaves of different sizes were collected from seven sites, dried at 80 °C for 48 h and weighed. We carried out a linear regression with leaf dry weight as the dependent variable and length of the middle leaflet of leaves as the independent variable. The best fitting model was obtained with logarithmically transformed data. The resulting equation was:

$$\text{Log}(y) = 1.98 (\pm 0.04 \text{ SE}) \times \text{log}(x) - 2.97 (\pm 0.14 \text{ SE})$$

$$(R^2 = 0.90, df = 277)$$

where *y* is the leaf dry weight (mg) and *x* is the length of middle leaflet (mm).

Classification of life-cycle stages and calculation of population projection matrices

In *F. vesca* as in many perennial plants, non-invasive age estimation based on above-ground morphological traits is not practicable. Furthermore, in many species reproduction

and reproductive output are dependent on body size, and size is often a better predictor of vital rates than age (Caswell 2001). We therefore distinguished the following life-cycle stages of plants:

1. Seedlings with a pair of cotyledons and usually one or two leaves.
2. Nodes (clonal offspring) produced on above-ground stolons.
3. Small adult plants (based on estimated biomass).
4. Large adult plants (based on estimated biomass).

Size class borders of adults were chosen in such a way that vital rates of every class could be calculated for each of the twelve sites, i.e., that there were plants present in all classes at every site at every census. Due to large differences in plant size structures between the 12 study sites it was not possible to use more than two size classes for adults. Plant size ranges differed strongly between spring, summer and fall and we chose different size class borders between small and large adult plants for spring (76 mg), summer (150 mg) and fall (92 mg). Numbers of plants in size classes at the different censuses are given in the ESM (S2).

Transition probabilities from one life-cycle stage to another were calculated for each stage as the proportion of individuals that have remained in that stage (stasis) or have changed to other stages (growth or retrogression) after a given time period (Fig. 1). In our model, seedlings and

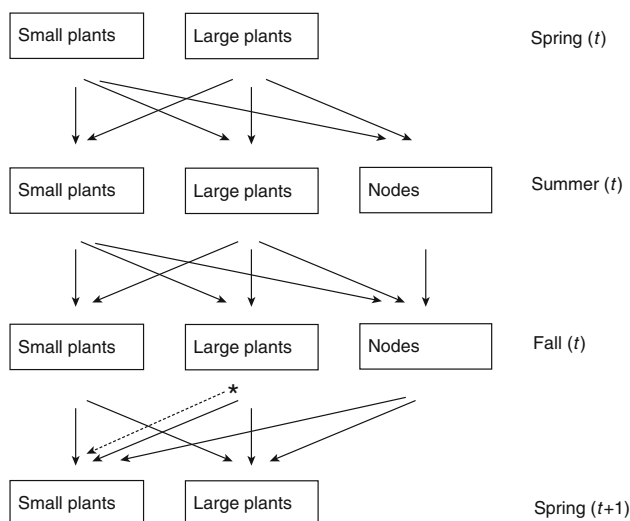


Fig. 1 A seasonal life cycle graph for *F. vesca* depicting transitions as used in the periodic matrix models. Each horizontal row represents a season of the year. Small and large plants may remain in their size class or change class and may reproduce clonally from spring till summer and from summer till fall. Clonally formed nodes may grow to small or large plants from fall to spring. Asterisk For our models sexual reproduction was defined as the number of seedlings found within plots per year and per number of large plants present, that grow to small plants from fall to spring

nodes were classified as either small or large adults in the spring following the year of their formation (Fig. 1). We did not include a seedling class in our population projection matrices because seedlings were very rare. Only 11 seedlings were found during the whole study, always in summer or fall. The effective sexual reproduction of adult plants was calculated as the annual number of seedlings detected that survived through winter divided by the number of large adult plants (Fig. 1). Survival and transition rates of seedlings were calculated from the pooled data of natural and planted seedlings. As the differences in the number of seedlings were very small between sites (0–3 seedlings per year and site) and seedling mortality was very high (see below) it was practical to use the highest rate of effective sexual reproduction found for all sites. In this way the highest rate of effective sexual reproduction could be used to estimate the importance of sexual reproduction for sites where no seedlings were found without the danger of significantly overestimating it. Clonal reproduction of adult plant classes was calculated as the mean number of nodes produced during each time period. We calculated separate matrices for parameters of (1) growth, stasis and retrogression (hereafter referred to as growth matrix B_G), (2) sexual reproduction (B_S) and (3) clonal reproduction (B_C) of plants; every element of B_G , B_S or B_C gives the transitions or contributions of individuals from a class at time t (column) to a class at time $t + 1$ (row). Summation of matrices B_G , B_S and B_C resulted in the population projection matrix B . For each year and site, vital rates were estimated for three seasonal periods, i.e., ‘spring–summer’, ‘summer–fall’ and ‘fall–spring’ and for each period a seasonal population projection matrix was calculated. These matrices were combined to a periodic matrix model to describe the population dynamics over an annual cycle (Caswell 2001):

$$A_{\text{spring}(t) \text{--} \text{spring}(t+1)} = B_{\text{fall}(t) \text{--} \text{spring}(t+1)} B_{\text{summer}(t) \text{--} \text{fall}(t)} B_{\text{spring}(t) \text{--} \text{summer}(t)}$$

Data analysis

All calculations and analyses were done in R (R Development Core Team 2009).

Survival and sexual and clonal reproduction of adult plants

We checked whether survival and reproduction were size-dependent in *F. vesca* to show that a modeling approach based on a classification of plants according to size was reasonable. Furthermore, habitat (i.e., forest or forest edge) was included as a factor in models of survival and reproduction.

The influences of plant size and habitat on plant survival from 1 year to the next and on probability of sexual (i.e.,

fruit production) and clonal reproduction were tested with generalized linear mixed models (function lmer using Laplace-method). Models were calculated with either survival, sexual reproduction or clonal reproduction as dependent binary variable, and estimated spring above-ground biomass as independent continuous variable and habitat as fixed effects. Because measurements from individuals within a site were not independent, we included site as a random effect.

Trade-offs between sexual and clonal reproduction

To detect trade-offs between sexual and clonal reproduction, we analysed whether annual fruit production of plants was correlated to their annual node production. A weighted measure of annual fruit production was calculated as:

Annual fruit production/Estimated spring above-ground biomass

We calculated generalized linear mixed models (function lmer using Laplace-method) with the total annual node production as Poisson-distributed dependent variable and the weighted annual fruit production and habitat as fixed effects. Site was treated as a random effect.

Seedling survival

To analyse whether the survival of natural seedlings and planted seedlings was similar, we used a generalized linear model with the proportion of seedlings surviving from time of germination till the spring of the following year as dependent variable and the seedling type (i.e., natural or planted seedling) as independent factor.

Lambda, stable stage structure and elasticity analyses

We calculated population growth rates λ and stable stage structures for the periodic matrix models of all sites and years. Stable stage structures calculated for the periodic matrix model for ‘spring 2009–spring 2010’ were compared to the observed stage structures found in spring 2009 using Keyfitz’s Δ . This standard measure quantifies the distance between stable and observed stage distributions with values ranging from 0 to 1, corresponding to maximum similarity and maximum difference, respectively (Caswell 2001).

Furthermore, we applied sensitivity and elasticity analyses to the seasonal population projection matrices. We followed the method for sensitivity analysis of periodic matrix models described by Caswell and Trevisan (1994). This method allows to analyse how λ over the entire annual cycle responds to changes in the vital rates at each season

within the cycle. Elasticities of λ to changes in the entries of a seasonal population projection matrix B are given by

$$E_B = (1/\lambda)B \circ S_B \quad (1)$$

where E_B and S_B are the elasticity and the sensitivity matrices of λ with respect to matrix B , respectively, and \circ denotes the Hadamard product (Caswell 2001). Some of the matrix elements of the seasonal population projection matrices were made up of different vital rates, e.g., the retrogression of large adult plants to small adult plants and seedlings becoming small adults in the ‘fall-spring’ matrices (S3 in ESM). To calculate elasticities of the different components of a seasonal population projection matrix B , we decomposed the seasonal matrix into three matrices (1) B_G , containing the rates of stasis, growth and retrogression, (2) B_S , containing the rates of sexual reproduction, and (3) B_C , containing the rates of clonal reproduction. To attribute elasticities of λ to elements of B_G , B_S and B_C we applied (1) to B_G , B_S and B_C separately. The elasticities of the composite elasticity matrix $E_B = E_{B_G} + E_{B_S} + E_{B_C}$ sum up to 1 for each season. Transition and elasticity matrices of B_G , B_S and B_C of all seasons and years are given in the ESM (S3).

Life table response experiment

In a LTRE the effect of a treatment, e.g., an environmental factor, on population growth rate λ is decomposed into contributions arising from the treatment effects on the different vital rates (Caswell 2001). This decomposition reveals the vital rates most responsible for the population level effect of the treatment retrospectively. Our models for survival, sexual reproduction and clonal reproduction showed that vital rates were influenced by habitat, i.e., forest or forest edge (see “Results”; Table 2a–c). Therefore, we performed a LTRE with habitat as treatment factor. We calculated differences in vital rates between habitats and how these differences contributed to differences in population growth rate λ . We calculated mean periodic transition matrices for forest sites (M_F) and forest edge sites (M_{FE}) for all periods in both years. As reference matrices we used the M_F -matrices. Matrices of differences for the different time periods were defined as

$$M_{D(ij)} = M_{FE(ij)} - M_{F(ij)}$$

where subscripts in parentheses denote the period (i) and the year (j). For the calculation of contribution matrices we worked out overall sensitivity matrices $M_{S(ij)}$ that were calculated from pooled data from all sites. Contribution matrices were then calculated as (Caswell 2001)

$$M_{C(ij)} = M_{D(ij)} \circ M_{S(ij)}$$

where \circ denotes the Hadamard product. The sum of the entries of the three contribution matrices of one annual

Table 2 Results of generalized linear mixed effect models for (a) survival, (b) sexual reproduction, (c) clonal reproduction and (d) total number of nodes in *F. vesca* in 2008 and 2009

	Test statistic	df	P
(a)			
Survival 08–09 ~ biomass spring 08 * habitat type			
Biomass	$t = 3.51$	928	<0.01
Survival 09–10 ~ biomass spring 09 * habitat type			
Biomass	$t = 4.03$	1098	<0.01
Habitat type	$t = 0.57$	10	0.29
Biomass × habitat type	$t = 2.55$	1098	<0.01
(b)			
Sexual reproduction 08 ~ biomass spring 08 * habitat type			
Biomass	$z = 7.42$	933	<0.01
Sexual reproduction 09 ~ biomass spring 09 * habitat type			
Biomass	$z = 9.60$	1089	<0.01
Habitat type	$z = 2.54$	10	0.01
(c)			
Clonal reproduction 08 ~ biomass spring 08 * habitat type			
Biomass	$t = 8.98$	933	<0.01
Habitat type	$t = 2.99$	10	<0.01
Biomass × habitat type	$t = 2.22$	933	0.013
Clonal reproduction 09 ~ biomass spring 09 * habitat type			
Biomass	$z = 10.98$	1089	<0.01
Habitat type	$z = 0.73$	10	0.46
Biomass × habitat type	$z = 3.71$	1089	<0.01
(d)			
Total nodes 08 ~ (total fruits 08/biomass spring 08) * habitat type			
No significant variables or factors			
Total nodes 09 ~ (total fruits 09/biomass spring 09) * habitat type			
No significant variables or factors			

For every model, the maximum model is given. Asterisk indicates inclusion of interactions between variables and factors. Site was included as a random effect in all models. Significant variables, factors and interactions are listed. Models with overdispersion were refitted using dispersion as scale parameter. Associated t values were then tested using Student’s t distributed error probabilities

cycle should closely approximate the difference between annual population growth rates λ of the different treatments.

Matrix entries of the seasonal population projection matrices were never composites of the growth matrices and the clonal reproduction matrices. Therefore, calculation of contribution matrices was straightforward and their entries could be assigned to single vital rates. Although some matrix entries of the ‘fall–spring’ seasonal projection matrices were composites of sexual reproduction matrix entries and entries of the growth matrix (S3 in ESM), sexual reproduction matrix entries had no influence on the values of the difference matrix as they were chosen to be identical for all sites in our model (see “Classification of life-cycle stages and calculation of population projection matrices”).

Results

Survival and sexual and clonal reproduction of adult plants

Above-ground biomass had a highly significant influence on survival, sexual reproduction and clonal reproduction in both

years (Table 2a–c). However, survival did not differ between forest and forest edge habitats in 2008 and in 2009, although there was a significant interaction for biomass and habitat in 2009. The probability of clonal reproduction was significantly increased for plants growing at forest edges in 2008, but was not affected by habitat type in 2009, although there was a significant interaction for biomass and habitat. Furthermore, plants from forest edges had a significantly increased probability of sexual reproduction in 2009 but not in 2008.

Trade-offs between sexual and clonal reproduction

We did not detect any significant effect of weighted annual fruit production on annual node production in both years (Table 2d). However, there was a marginally significant negative correlation between weighted fruit production and node production in 2009 ($t_{1089} = -1.52, P = 0.064$).

Seedling survival

Only 11 natural seedlings were found during the whole study, always in summer or fall, and 2 seedlings (18 %)

survived their first winter. In 2008, six natural seedlings were found which all died within a year. In 2009, five natural seedlings were found of which one survived till spring 2010. The survival of the planted seedlings was even lower. Of the 960 seedlings that were planted only 7 (0.7 %) survived their first winter. None of the 480 seedlings planted in 2008 survived till spring 2010 and four of the 480 seedlings planted in 2009 were still alive in spring 2010. The proportion of natural seedlings that survived their first winter was significantly higher than the proportion of planted seedlings ($z_{1,969} = -3.94$, $P < 0.01$).

Lambda, stable stage structure and elasticity analyses

Mean population growth rates λ for the two periodic matrix models ‘spring 2008–spring 2009’ and ‘spring 2009–spring 2010’ were 1.61 and 0.28, respectively, and had a large range with extreme minimum and maximum values of 0.03 and 6.08 (Table 1). At all sites, λ was smaller for the period ‘spring 2009–spring 2010’ and well below 1 with the exception of one site.

Keyfitz’s Δ values for stable size distributions calculated for the periodic matrix model ‘spring 2009–spring 2010’ and the size distributions observed during the exhaustive census in spring 2009 were low, showing that actual size

distributions were generally close to stable size distributions (S4 in ESM).

To present an overview of the relative importance of plant survival and clonal reproduction for population growth, we summed up (1) elasticities of λ to changes in the growth matrices for adult plants (small and large) and for nodes separately and (2) elasticities of λ to changes in the clonal reproduction matrices of adult plants (Fig. 2). Elasticities of λ to changes in the sexual reproduction matrices of adult plants were low and never exceeded 1 % (S3 in ESM). In general, largest elasticities were found for survival of adult plants (mean for pooled data 63 %, range 16–100 %), but in a few cases elasticities were largest for survival of nodes (mean for pooled data 34 %, range 2–84 %). Elasticities of λ to changes in clonal reproduction were high (mean for pooled data 22 %, range 1–44 %), especially in 2008. Complete elasticity matrices are given in the ESM (S3).

Life table response experiments

For presentation, we added up projection matrix element differences and contributions for small plants, large plants and clonal offspring separately (Fig. 3); note that the sum of contributions of growth matrix entries yields the overall contribution of plant survival.

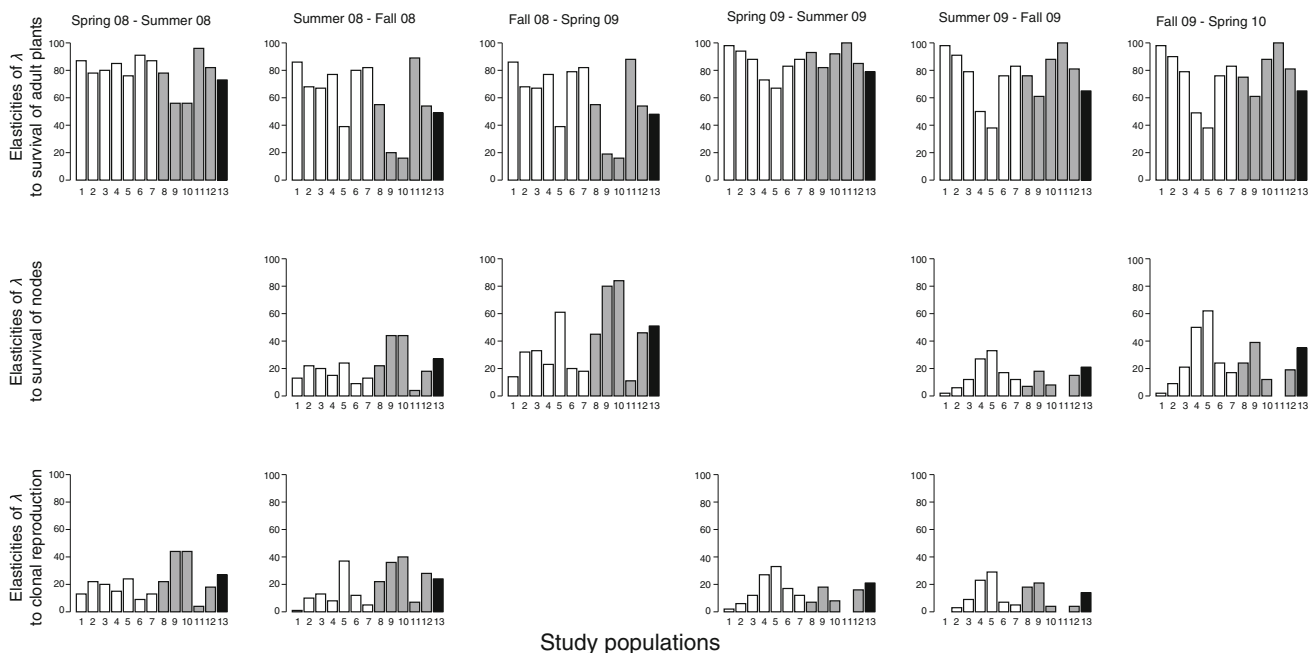


Fig. 2 Elasticities of λ of periodic matrix models of natural *F. vesca* populations for spring 2008 to spring 2010 to changes in survival of adult plants (small and large), survival of nodes and clonal reproduction of adult plants. Elasticities are given as rounded percent values. Elasticities of λ to changes in sexual reproduction of adult plants never exceeded 1 % and are not shown. Note that no nodes were present in spring. No clonal reproduction takes place from fall to

spring and there are no respective diagrams. *White bars* represent forest populations, *grey bars* represent forest edge populations and *black bars* represent values for pooled data from all sites. 1 Adlerberg, 2 Eichmatt, 3 Gempen, 4 Grammet, 5 Schauenburg, 6 Schleifenberg, 7 Ziefen, 8 Holzenberg, 9 Hochwald, 10 Paradies, 11 Riehen, 12 Scharten, 13 all sites

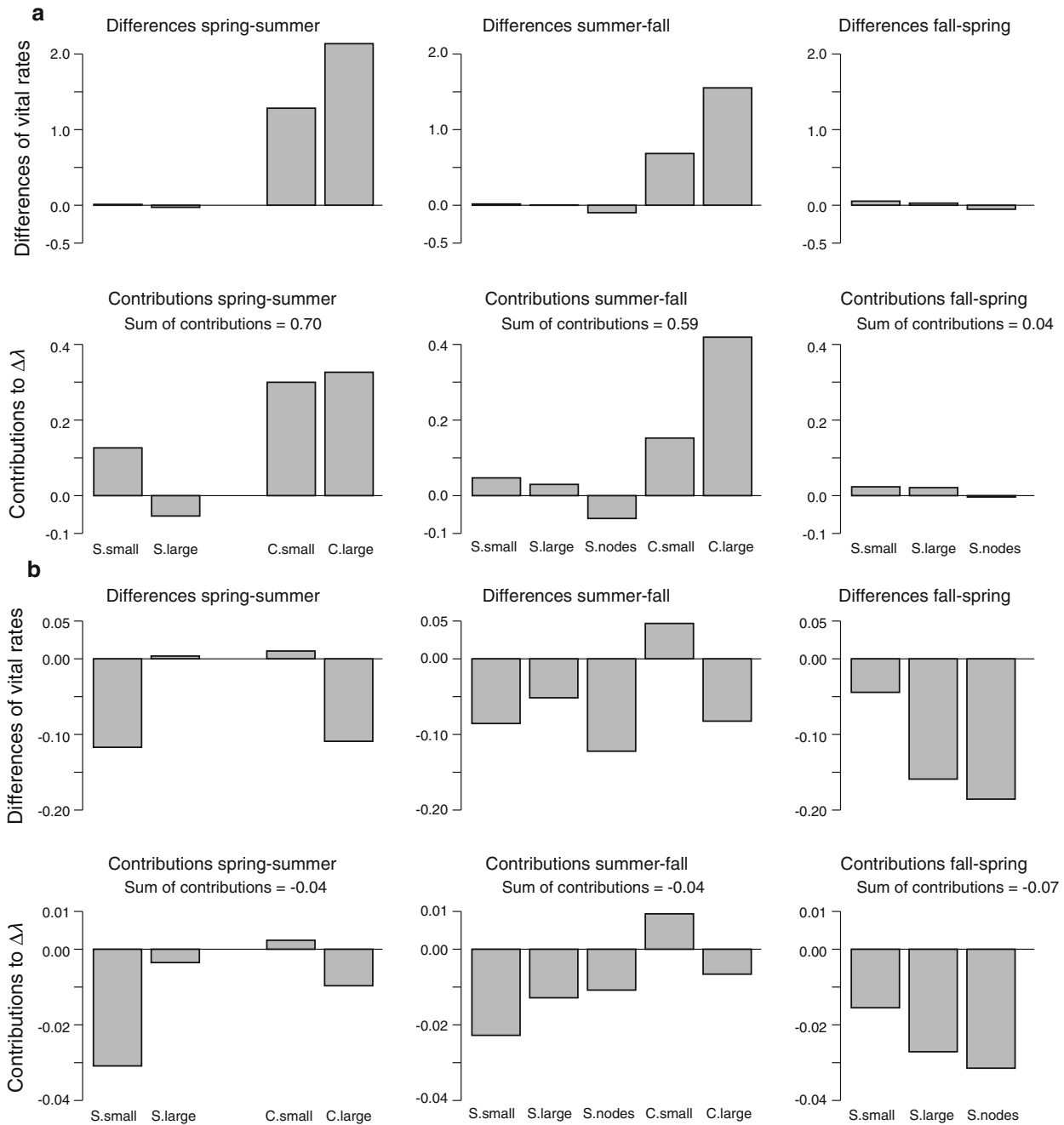


Fig. 3 Differences of vital rates of *F. vesca* plant stages between the mean seasonal population projection matrices of forest and forest edge populations and contributions of differences in vital rates to differences in λ for the periods ‘spring 2008–spring 2009’ (a) and ‘spring 2009–spring 2010’ (b). Mean forest population projection matrices were used as reference matrices. Note that clonal

reproduction started later in the year and there were no clonal offspring survival rates for season ‘spring–summer’. Note different axis-scales in a and b. *S.small* survival of small plants, *S.large* survival of large plants, *S.nodes* survival of clonal offspring, *C.small* clonal reproduction of small plants, *C.large* clonal reproduction of large plants

2008–2009

Population growth rates λ for the period ‘spring 2008–spring 2009’ were 1.21 and 2.48 for mean periodic matrix models of forest and forest edge habitats, respectively. The largest differences between elements of seasonal projection

matrices of forest and forest edge habitats were found for clonal reproduction rates in summer and fall (Fig. 3). Differences in clonal reproduction also contributed most to differences in λ . Contributions of clonal reproduction to differences in λ added up to 1.20. Differences in survival of adult plants were small but they yielded relatively high

contributions to differences in λ that added up to 0.19. Adult plant survival was always higher at forest edges with the exception of large plants during the period ‘spring 2008–summer 2008’. On the other hand, survival of clonal offspring was worse at forest edges and survival contributions to differences in λ added up to -0.06 .

The difference in λ between forest and forest edge habitats was 1.27. The total of contributions of the three seasonal contribution matrices was 1.33.

2009–2010

Contrary to the previous year, λ for the period ‘spring 2009–spring 2010’ was lower for forest edges (0.18) compared to forests (0.33). Clonal reproduction was very low at most sites and differences between seasonal projection matrices of forests and forest edges were small (Fig. 3). Similarly, contributions of clonal reproduction to differences in λ were small and added up to -0.005 . Adult plant survival was mostly lower at forest edges. Generally, differences in adult plant survival were larger than in the previous year, but contributions to differences in λ were relatively small, adding up to -0.11 . Differences in survival of clonal offspring were similar to the previous year as were the contributions to differences in λ that added up to -0.04 .

The difference in λ between forest and forest edge habitats was -0.15 . The total of contributions of the three seasonal contribution matrices was -0.16 .

Discussion

Vital rates of *F. vesca* varied considerably between sites and years but the mean results of elasticity analyses clearly indicate that clonal reproduction is the dominant reproductive pathway in established populations. Elasticities of λ to changes in clonal reproduction or to changes in the survival of nodes even surpassed elasticities of λ to changes in survival of adult plants for some sites and periods. A comparison to the elasticities of λ to changes in clonal reproduction of 25 other clonal herbs (range 1–25 %, Silvertown et al. 1993) shows that our *F. vesca* values are relatively high. The observed strong influence of clonal reproduction on population growth in *F. vesca* can be explained by the high survival rates of nodes, which were often similar to the rates of adult plants, and the fast growth of nodes. Nodes can reach the size of adult plants within the year of their creation, and we have observed nodes that flowered during the year of their creation although this is not common. In contrast to the importance of clonal reproduction, elasticities of λ to changes in sexual reproduction were insignificant. These findings are in line with

two older studies on wild strawberry populations in which no *F. vesca* seedlings were found (Angevine 1983; Jurik 1985). Sexual reproduction in *F. vesca* may rather serve as a mechanism for dispersal to new sites than for reproduction within established populations. Indeed the red fleshy fruits of *F. vesca* suggest an adaptation to endozoochorical seed dispersal, and mammals, birds and slugs have been described as seed dispersal mutualists of *Fragaria* spp. (Müller-Schneider 1986; Willson 1993). However, seedling recruitment rates of a few years may not be representative for long-term population dynamics. As successful seedling recruitment may occur only sporadically over longer time periods (Crawley 1990; Eriksson and Ehrlén 2008) such events are easily missed. For example, one of the longest studies of perennial plant populations showed that periods of about a decade elapse between seedling recruitment events in the forest herb *Hepatica nobilis* Mill. (Ranunculaceae) (Inghe and Tamm 1985). ‘Safe sites’ that provide the conditions required for seedling recruitment are a limiting factor for recruitment (Harper 1977; Eriksson and Ehrlén 2008). Therefore, successful seedling recruitment in *F. vesca* may depend on disturbance events (e.g., soil upheaval, trampling) that create new safe sites. Disturbance can also lead to seedling recruitment from seeds persisting in the soil seed bank (Harper 1977) although persistence of *F. vesca* seeds seems to be low. In a database on soil seed banks ten, five and two studies classify *F. vesca* seeds as transient (<1 year persistence), short-term persistent (1–5 years persistence) and long-term persistent (>5 years persistence) in the soil seed bank, respectively (Thompson et al. 1997). However, we did not notice any disturbance in our study plots that could have promoted seedling recruitment.

Models for sexual and clonal reproduction show that both are influenced by habitat type. Forest edge habitat had a positive effect on sexual (in 2009) and clonal reproduction (in 2008). Furthermore, there was a significant interaction between biomass and habitat type for clonal reproduction in 2008 and 2009. Therefore, population dynamics in the two habitats can be expected to differ. We attribute this habitat effect to the differences in light availability. Previous studies have shown that with increasing light availability an increasing fraction of carbon is allocated to sexual and clonal reproductive structures in *F. vesca* (Chabot 1978; Jurik 1983) and that variation in light availability, as compared to variation in temperature and nutrient supply, has the strongest effect on plant growth (Chabot 1978).

The results of our LTRE show a different habitat effect on population dynamics in the 2 years. In the period ‘2008–2009’, population growth rate λ was higher in the forest edge habitat, and clonal reproduction was the vital rate contributing most to the difference in λ . In the period

‘2009–2010’, population growth rate λ was lower in the forest edge habitat, and low survival rates contributed most to the difference in λ . We attribute habitat effects to differences in light availability but it is not yet clear in what way light availability may have caused differences in population dynamics.

Differences in population dynamics among habitats are either caused by abiotic or biotic environmental conditions or a combination of the two. Regarding abiotic environmental conditions, the analysis of precipitation data showed considerably lower precipitation in 2009 during periods important for plant growth and clonal reproduction and provides some evidence of differences in water availability between years. Our results indicate that a habitat type is not per se favourable or unfavourable. Rather a habitat characteristic can prove to be beneficial or adverse for population growth under different environmental conditions. Here, the habitat characteristic of increased light availability in the forest edge habitat seems to have had a positive effect on clonal reproduction under sufficient water availability and a negative effect on plant survival under relatively dry conditions. Biotic environmental conditions, i.e., density and size of conspecific and heterospecific plants and plant community composition, also varied within and between habitats, and intraspecific competition or competition through plant succession may have influenced population dynamics. However, data on heterospecific plant neighbours, plant community composition and various abiotic conditions, e.g., foliage-layer, soil type and nutrient availability, within study plots were not recorded. Therefore, the effects of inter- and intraspecific competition and abiotic conditions on population dynamics could not be traced. Nevertheless, populations with high growth rates in the first year may have had declining growth rates in the following year due to intraspecific competition or resource depletion. Furthermore, a major difficulty in the study of plant populations is that the majority of species are successional (Crawley 1990). Successional change in natural plant communities may be the rule rather than the exception. Local plant populations often go extinct during the course of a study as the environmental conditions favouring plant recruitment are no longer met within the plots where the initial cohort of adult plants was selected (Crawley 1990). Therefore, declining growth rates of our *F. vesca* populations may simply reflect local changes in species composition and abundance after an initial population growth of *F. vesca* under favourable conditions. To solve this fundamental problem it has been proposed to include demographic data from newly occupied sites by including ‘empty quadrats’, i.e., potentially habitable sites from which the species is currently missing, from the outset of the study (Crawley 1990). This approach will certainly be appropriate in many situations but its

usefulness will depend to some extent on the life strategy of the studied species and may not solve the problem for studies that last only 2 or 3 years.

No significant trade-offs between sexual and clonal reproduction were found. However, there was a marginally significant negative effect of fruit production on node production in 2009, which suggests the operation of a trade-off. Trade-offs may be difficult to detect in field studies, as plots may not be homogeneous enough in time and space to detect trade-offs between fruit and node production, especially as sexual and clonal reproduction in *F. vesca* are temporally separated for the most part. However, trade-offs between sexual and clonal reproduction have been reported from observational field studies (Worley and Harder 1996), whereas in other cases no trade-offs were found in experimental studies under controlled conditions (Reekie 1991; Thiele et al. 2009).

In conclusion, *F. vesca* relies heavily on clonal reproduction for local population growth. Furthermore, reproduction and the survival of different life stages and their relative importance for population growth depend highly on spatio-temporal variation of environmental conditions. However, if the landscape level is considered, i.e., the pooled data from all sites, elasticities of λ to changes in the vital rates of different years are relatively similar. This shows that extreme conditions at the site scale can balance out at the landscape level and that the inclusion of spatial variability is absolutely necessary to obtain a reasonably objective picture of the general demography of a species.

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