Environmental heterogeneity, population dynamics and life-history differentiation in *Primula farinosa*

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Environmental heterogeneity, population dynamics and life-history differentiation in *Primula farinosa*

**Abstract** - Allocation to reproduction is a key life-history trait. Optimal allocation to reproduction depends on environmental conditions because of their effects both on costs and benefits of reproduction and on patterns of growth, fecundity, and mortality. In this thesis, I studied 24 populations of the perennial herb *Primula farinosa* in the northern part of the Great Alvar on Öland, SE Sweden, and in an experimental garden at Stockholm University to investigate how plant allocation patterns and population dynamics vary along environmental gradients. In the first study, I performed experimental manipulations of reproduction to study costs of reproduction in relation to water availability. In the second study, I performed a demographic survey to investigate the effects of pre-dispersal seed predation on host-plant population dynamics in relation to environmental context. In the third study, I used a common garden experiment to investigate whether environmental variation among natural populations was correlated with genetic differentiation in reproductive effort, and in the fourth study, I performed reciprocal transplantations among four populations to investigate whether genetically based adaptive differentiation among local populations could be detected. The results showed that under natural conditions, plant reproductive costs, intensity of pre-dispersal seed predation, population growth rate and reproductive effort varied with water availability and vegetation height. Costs of reproduction were detected at high and low water availability but not under intermediate soil moisture conditions (paper I). Population dynamics of *P. farinosa* were affected by environmental conditions both directly, through effects on potential population growth rate (in the absence of seed predation) and indirectly, through effects on seed predation intensity and sensitivity to seed predation (paper II). Among-population genetic differentiation in reproductive allocation was documented in the common-garden experiment (paper III). However, reciprocal transplantations among populations separated by up to 6.2 km provided no evidence of local adaptation to current environmental conditions. Moreover, large differences in the performance of individuals transplanted to different study sites suggest that the study populations display considerable phenotypic plasticity (paper IV). Taken together, the results of these studies suggest that environmental variation has important direct and indirect effects on population dynamics and life history trade-offs in *P. farinosa*, and that differences in reproductive effort partly reflect genetic differentiation, but that phenotypic variation observed among natural populations does not reflect adaptations to current environmental conditions.

**Key-words:** Biotic interactions, Demography, Environmental heterogeneity, Genetic differentiation, Life-history traits, Local adaptation, Plant-herbivore interactions, *Primula farinosa*, Resource allocation
List of papers

This thesis is based on the following papers, which are referred to by their roman numerals:


II. von Euler, T., Ågren, J. & Ehrlén, J. Environmental context influences the impact of pre-dispersal seed predation on host plant population dynamics in multiple ways. *Manuscript*

III. von Euler, T., Ågren, J. & Ehrlén, J. Genetic differentiation in reproductive effort in the perennial herb *Primula farinosa* is related to vegetation height. *Manuscript*

Introduction

Life-histories influence the ability of organisms to survive under given environmental conditions, and environmental heterogeneity may result in divergent selection on life-history traits (Silvertown et al. 1993; Bazzaz 1996; Roff 2002). Spatial variation in plant population dynamics has been related to environmental factors such as nutrient availability (Gotelli & Ellison 2002; Brys et al. 2005; Dahlgren & Ehrlén 2009), management regime (Lindborg & Ehrlén 2002; Quintana-Ascencio et al. 2009; Sletvold et al. 2010), and water availability (Casper 1996; Eckstein 2005; Schleuning, et al. 2008; Toräng et al. 2010). Also, biotic interactions are often of fundamental importance to plant population dynamics. These interactions may be mutualistic, such as plant-pollinator interactions, or antagonistic, such as plant-herbivore interactions and inter- or intraspecific plant-plant competition (e.g. Waloff & Richards 1977; Aker 1982; Rose et al. 2005; Yang et al. 2011). Furthermore, the impact of biotic interactions on plant population dynamics may vary with environmental context (Münzbergová 2006; Kolb et al. 2007). Thus, plant population dynamics may be both directly and indirectly affected by environmental conditions; directly via effects on potential population growth rate, and indirectly via effects on the intensity of biotic interactions and on the sensitivity of population growth rates to these interactions.

Habitat quality influences not only plant population dynamics, but also optimal allocation to reproduction. Spatial variation in habitat quality may greatly affect plant resource acquisition and allocation. In perennial plant species, high reproductive allocation may result in high reproductive success, but may also result in increased reproductive costs, for instance in terms of reduced future reproduction (Snow & Whigham 1989; Primack & Hall 1990; Newell 1991; Andersson 2006; Sletvold & Ågren 2011). Reproductive costs often depend on habitat conditions influencing resource-availability, and reproductive costs are often more prominent in stressful environments (Primack & Antonovics 1982; Tuomi et al. 1983; Galen 2000; Hultine et al. 2007, but see Hemborg & Karlsson 1998). Thus, the optimal allocation between growth and reproduction should depend on habitat quality (Jurik 1985; Reekie 1998).

Given that optimal allocation to reproduction depends on mortality and recruitment rates, environmental conditions will influence optimal allocation both via effects on mortality and recruitment and via resource availability. According to life history theory, variation in mortality regimes should contribute to variation in reproductive strategies. When mortality is size-dependent, organisms should benefit from attaining a large size to increase the chances of survival, whereas in environments where mortality is unpredictable and less size-dependent, it should be favorable to start reproducing early and allocate more resources to reproduction, to maximize life-time reproductive success (Williams 1966; Stearns 1976; Roff 2002). For example, high size-independent mortality rates due to grazing and trampling by large herbivores should select for high allocation to reproduction in plants. In contrast, in areas of tall or dense vegetation and where plant-plant competition is high, allocation to growth at the expense of reproduction should be favored (Harper 1967; Grubb 1977; Fisher & Matthies 1998). Another factor that may greatly influence plant performance is water availability, and periods of severe drought are often associated with high size-independent mortality and subsequent opportunities for recruitment (e.g. Edwards & Crawley 1999; Otsus & Zobel 2004; Toräng et al. 2010), which should also favor a higher reproductive allocation.
If differential selective pressures persist over time, they may eventually result in adaptive genetic differentiation among plant populations. Whether genetic differentiation actually evolves depends on available genetic variation, the spatial scale of environmental heterogeneity and gene flow (Via & Lande 1985; Van Tienderen 1991; Kawecki & Ebert 2004). Whereas adaptive genetic differentiation may evolve between populations subject to persistent divergent selection, phenotypic plasticity should be favored in response to predictable temporal variation in the environment and where the change in the affected trait keeps pace with the environmental change (e.g., Bradshaw 1965; Alpert & Simms 2002).

Reciprocal transplant experiments, which involve transplanting plants of different origin between two or more sites, are often used to investigate whether plant populations are locally adapted to current habitat conditions (Kawecki & Ebert 2004). If populations are locally adapted, local plants should outperform non-local plants. Most reciprocal transplant experiments of perennial plants have been based the documentation of one or few components of fitness, rather than total fitness (but see Rice & Mack 1991; Becker et al. 2006). However, because natural selection acts on total fitness and because the impact of single fitness components on total fitness may vary between environments, assessments of local adaptation should preferably be based on effects integrated over the entire life cycle.

Aim of the thesis

The aim of this thesis was to investigate how reproductive allocation and population dynamics are influenced by environmental context in terms of abiotic factors and biotic interactions, and whether variation in environmental conditions have resulted in genetic differentiation among populations of the perennial herb Primula farinosa (Fig 1). I asked the following questions: Do costs of reproduction differ among habitats and among individuals with different reproductive traits? (paper I), Does environmental context influence population growth rates, intensity of seed predation and sensitivity of population growth rates to seed predation? (paper II), Is environmentally induced variation in demographic rates correlated with genetic differentiation in reproductive effort among populations? (paper III) and Does genetic differentiation among populations reflect local adaptation to prevailing habitat conditions? (paper IV).
Methods

Study system
As study system, we used *Primula farinosa* L. (Primulaceae), bird’s-eye primrose. *P. farinosa* is a small, rosette-forming, distylosous, perennial herb. It usually flowers in May and fruiting takes place in July. It occurs in moist calcareous grasslands and its distribution ranges from central Sweden and Scotland to central Spain and Bulgaria (Tutin 1972). It is pollinated mainly by butterflies and solitary bees, and fruits are sometimes attacked by the seed predator moth *Falseuncaria ruficiliana*. In some areas (including our study area), *Primula farinosa* occurs in two scape morphs. Alongside the common long-scape morph, with a scape-length of 5–20 cm, there exists a shorter, nearly scape-less morph, with a thick, striate scape of up to 3 cm (Lagerberg 1957; Fig 2). Previous studies have found that plants of the shorter scape morph are more pollen-limited than plants of the taller scape morph. However, individuals of the shorter morph more often escape seed predation and grazing by cattle (Ehrlén *et al.* 2002; Ågren *et al.* 2006; Vanhovenacker *et al.* 2009). The studies were performed in the northern part of the Great Alvar on the island Öland, SE Sweden, and in an experimental garden at Stockholm University. The great Alvar is characterized by thin calcareous soils that are often flooded in the spring and become very dry in the summer, and large parts of the area are grazed by cattle, sheep and horses (Rosén 1995; Ekstam 2002).
Figure 2. Long-scaled and short-scaled morph of *Primula farinosa* on the Great Alvar, Öland, Sweden. Photo: Veronika Johansson.

Figure 3. The twenty-four populations of *Primula farinosa* located within an area of 40 Km$^2$ in the northern part of the Great Alvar, Öland, Sweden, that were used for this study.
**Experimental design and outline of analyses**

Data were collected during a period of four years, 2007-2011. Twenty-four *P. farinosa* populations within an area of 40 km² were used for the analyses (Fig 3). The study sites varied in soil depth, which affects water availability and vegetation cover, and grazing intensity, which should affect vegetation height and disturbance (Fig 4). To investigate cost of reproduction in relation to habitat quality and floral display (paper I), experimental manipulation of reproduction, by means of flower and bud removal at the onset of flowering, was performed in eight of the study populations, and the effect of treatment on future performance, in terms of growth and flower production, was examined in the following year. To study how the impact of seed predation intensity on population growth rate depended on environmental context (paper II), permanent plots were established in each of the 24 populations and yearly recordings of survival, rosette diameter, reproductive status (flowering vs. non-flowering), scape morph, number of flowers and fruits, grazing (0 or 1) and seed predation (proportion of fruits consumed) for each individual were made during four consecutive years and incorporated into integral projection models exploring the effect of seed predation. To examine whether among-population variation in reproductive effort observed in the field represented genetic differentiation, a common-garden experiment was performed in which seeds were collected from 20 populations and grown in an experimental garden at Stockholm University for three consecutive years. Among-population differences in reproductive effort were documented and related to reproductive effort and environmental conditions at the sites of origin (paper III). To investigate whether Alvar populations of *P. farinosa* were locally adapted, we performed reciprocal transplantations between four populations, separated by up to 6.2 km. Plants of three different life stages were transplanted to the four sites and measures of survival, rosette diameter, probability of flowering and fruit production were used to estimate total fitness in terms of population growth rate using size-structured integral projection models (paper IV).
**Environmental variables**

Environmental variables were measured at the study sites in 2007-2010. Vegetation height was measured in July each year 2007-2010. At each site, measurements were taken in the vicinity 30 flowering individuals at each site. Three measurements were taken at each plant. Because site-specific means of vegetation height were highly correlated among years, we used site means of yearly means for statistical analyses. Soil depth and soil moisture were measured during two consecutive days in July 2010. Soil depth was measured by pushing a steel rod into the soil until it hit bedrock. Soil moisture was measured using a Theta Probe sensor connected to a HH2 moisture meter (Delta-T Devices Ltd). 16 measurements of soil depth and soil moisture, respectively, were taken at each site, and mean values of soil depth and soil moisture from each site were used in the statistical analyses. Because of between-year differences in precipitation and evaporation, absolute levels of soil moisture are likely to vary among years. However, since soil moisture is closely related to factors such as topography and soil depth and composition, we judged the ranking in soil moisture between study populations to be similar among years. For soil nutrient analyses, nine soil samples were collected at each site in May 2008. The samples were then pooled and analyzed for phosphorous, potassium, calcium and magnesium using the Al extraction method and total amounts of carbon and nitrogen. Analyses were carried out at the Division of Soil Fertility and Plant Nutrition at the Swedish University of Agricultural Sciences (SLU).

**Figure 4.** Three common environments for *Primula farinosa* on the Great Alvar, Öland. a) Dröstorp: thin soil, low moisture and sparse vegetation, b) Lenstad: deep soil, intermediate soil moisture, low vegetation, c) Torskulle: deep soil, high soil moisture, tall vegetation. Photo: Tove von Euler.
Data analysis
We investigated costs of reproduction by quantifying the effect of experimental flower and bud removal in the first year on growth and flower production in the following year. Cost of reproduction was analysed using generalized linear model Anovas of rosette size and number of flowers in response to flower removal treatment, population and scape morph. To assess the effect of water availability on the cost of reproduction, I regressed cost of reproduction (quantified as the ratio between number of flowers of manipulated individuals and the number of flowers of unmanipulated individuals in the year following treatment, analysis based on population means) on water availability using polynomial regression (paper I). In the second paper, The impact of seed predation on population growth rate was assessed by comparing integral projection models of population growth rates based on potential seed production (potential population growth rates), assuming that fruits subject to predation contained as many seeds as intact fruits, with models based on realized seed predation (realized population growth rates), assuming that attacked fruits contained no viable seeds. Effects of environmental context in terms of soil depth, soil moisture, soil nutrient availability and vegetation height on potential population growth rate, seed predation intensity and sensitivity of population growth rate to seed predation were examined using Lasso regressions (paper II). Among-population variation in reproductive effort in the field and in the common-garden experiment was analysed using linear mixed effect models (lmer). The effects of vegetation height and soil moisture on population means adjusted for differences caused by differences in scape morph frequencies among populations of reproductive effort were analysed using multiple regressions (paper III). In the reciprocal transplant study, effects of site and population of origin on survival, growth and probability of flowering were analysed using two-way Anovas. Population growth rate of experimental populations of each site × origin combination was estimated using integral projection models (paper IV).

Results

Overall results
In this thesis, I found differences in cost of reproduction, population dynamics and reproductive effort among populations of *P. farinosa*. Reproductive costs were non-linearly related to soil moisture; the lowest costs were detected at intermediate soil moisture conditions. I also found that cost of reproduction and reproductive effort were higher in long-scape than in short-scape individuals in the field. Moreover, potential population growth rates, intensity of seed predation and the sensitivity of population growth rates to seed predation were influenced by environmental context. The results of the common-garden experiment suggest that there is genetic differentiation among populations with regard to reproductive effort. However, the reciprocal transplant experiment did not reveal any evidence of local adaptation among four populations separated by up to 6.2 km.

*Paper I – Floral traits and habitat quality affect cost of reproduction in Primula farinosa.*
The results of the first study revealed reproductive costs in terms of reduced flower production in the year following reproduction. However, survival and rosette area in the following year did not differ between manipulated and unmanipulated individuals. Both reproductive investment, in
terms of fruit:flower ratio, and cost of reproduction differed between scape morphs. Analyses showed that long-scape plants had a higher fruit:flower ratio than short-scape plants and that flower removal increased flower production in the following year in the long-scape morph, but not in the short-scape morph. Moreover, the relationship between soil moisture and cost of fruit production differed between scape morphs. In long-scape plants, the cost of fruit production in terms of reduced flower production in the following year was significantly nonlinearly related to soil moisture. A cost was detected both at high and low levels of soil water content, but was absent at intermediate levels. In short-scape plants, there was no relationship between soil moisture and cost of fruit production.

_Paper II – Environmental context influences the impact of pre-dispersal seed predation on host plant population dynamics in multiple ways._

Realized population growth rates in _P. farinosa_ ranged from 0.60 to 1.97 and were related to environmental context both directly, via effects on potential population growth rate, and indirectly, via pre-dispersal seed predation. Moreover, the impact of pre-dispersal seed predation on population growth rates varied with both predation intensity and with sensitivity of population growth rates to seed predation. Potential population growth rate, predation intensity and sensitivity of population growth rate to seed predation were all negatively correlated with soil moisture, and potential population growth rate was also negatively correlated with vegetation height. No direct relationship was found between predation intensity and realized population growth rates.

_Paper III – Genetic differentiation in reproductive effort in the perennial herb Primula farinosa is related to vegetation height._

In the field and in the common-garden experiment, reproductive effort differed significantly among populations and this variation could partly be related to environmental variation at the sites of origin. In the common-garden experiment, among-population differences were also found in terms of size at first reproduction, whereas number of flowers or age at first reproduction did not differ among populations. In the field, reproductive effort was negatively related to both vegetation height and soil moisture. In the common garden, reproductive effort was negatively related to vegetation height, but not to soil moisture. Soil moisture and vegetation height values were not correlated with each other across the study populations.

_Paper IV – A demographic assessment of local adaptation in a grassland perennial herb._

In this study, we detected large effects of transplant site on plant performance, but we also detected effects of population of origin in several cases. Interaction effects between transplant site and population of origin were few. Survival differed mainly among transplant sites, with one site having consistently lower survival than the others. Growth varied significantly among sites and populations of origin. Moreover, we found an interaction between the effects of site and origin on growth. At one site, growth was significantly higher among plants originating from the local population. The proportion of plants flowering varied both among sites and populations of origin. Plants originating from two of the study populations had consistently lower flowering frequencies than plants originating from the other two populations. The effect of population of origin on fruit production per reproductive individual varied among sites. The percentage of reproductive plants grazed varied with site and origin. The relative ranking of the different populations at the transplant sites differed depending on which fitness component was considered and total fitness, in terms of population growth rate, showed no evidence of home site advantage.
Discussion

The results of the studies included in this thesis indicate that the performance of *Primula farinosa* is affected by spatial variation in environmental conditions in several ways. The first study suggests that under intermediate soil moisture conditions, reproductive investment does not incur considerable costs. However, under drought or water-logging conditions, reproduction occurs at the expense of future reproduction. Previous studies have documented variation in reproductive costs in response to environmental parameters such as soil fertility, water availability, temperature and light conditions (Biere 1995; Galen 2000; Sandvik 2001; Jacquemyn *et al.* 2010). The fact that reproductive costs were low at intermediate soil moisture conditions further supports the idea that reproduction should be more costly in stressful environments (Tuomi *et al.* 1983; Reekie & Bazzaz 1987). Moreover, both reproductive investment, in terms of fruit:flower ratio, and cost of reproduction differed between scape morphs. The fact that long-scaped individuals had a higher fruit:flower ratio is probably because they are less pollen limited than short-scaped individuals, being more conspicuous to pollinators (Ehrlén *et al.* 2002; Ågren *et al.* 2006; Vanhoenacker *et al.* 2009). Increased reproductive costs in response to high reproductive investment have been documented in previous studies (Snow & Whigham 1989; Galen 2000; Reekie *et al.* 2002). Differences between scape morphs in cost of reproduction may result in differences in the optimal reproductive allocation. Unless the benefits of reproduction exceed the costs, lower reproductive allocation may be favored in response to high reproductive costs. However, because of variation in resource availability and reproductive success, the relative difference in reproductive investment between the two scape morphs is likely to vary spatially and temporally, and reproductive costs will depend on environmental context affecting both resource availability and patterns of reproductive allocation (paper I).

In the second paper, I documented variation in population dynamics in relation to abiotic and biotic habitat conditions. The results showed that both predation intensity and sensitivity of population growth rate to reductions in seed production explained reductions in population growth rates due to seed predation. Moreover, the sensitivity of population growth rate to seed predation was higher at high potential population growth rates. High sensitivity to changes in fecundity at high population growth rate has been documented in previous studies (e.g., Silvertown *et al.* 1993; Horvitz & Schemske 1995; Ramula *et al.* 2008). Moreover, spatial variation in the sensitivity to reductions in seed production have been documented in previous studies (Ehrlén 1996; Münzbergová 2006; Kolb *et al.* 2007), which further indicates that the relationship between predation and realized population growth rate may not always reflect the strength of biotic interactions. Interestingly, water availability affected population growth rate both positively and negatively; potential population growth rate, the intensity of seed predation and the sensitivity of population growth rate to seed predation were all negatively associated with water availability and no direct relationship was found between predation intensity and reductions in population growth rate. Thus, environmental context affects population dynamics both directly, via potential population growth rate, and indirectly, via biotic interactions (paper II).

According to life history theory, selection should favor higher reproductive effort in environments of high adult mortality, where the probability of surviving to the next reproductive season is low (Williams 1966; Stearns 1976; Roff 2002). Thus, for plant populations exposed to
intense grazing and trampling or periods of extensive drought, high allocation to reproduction should be favored whereas at sites of low disturbance and adequate soil moisture conditions, mortality should be largely size-dependent and high allocation to growth may be favored. In the third study, I found that reproductive effort differed significantly among populations in a common garden experiment. At the sites of origin, reproductive effort was negatively related to vegetation height; plants growing in low vegetation had a higher reproductive effort than plants growing in tall vegetation. Moreover, reproductive effort was negatively related to soil moisture. Also in the common-garden, reproductive effort was negatively correlated with vegetation height at the sites of origin. However, whereas reproductive effort was also negatively related to soil moisture at the sites of origin, this pattern was not observed among the populations in the common-garden experiment, suggesting that variation in reproductive effort in response to soil moisture largely represents phenotypic plasticity (paper III).

Among-population genetic differentiation may be the result of divergent selection caused environmental heterogeneity (e.g., Galloway 1995), but may also result from genetic drift, especially in small, isolated populations (e.g., Ellstrand & Elam 1993). To correctly evaluate whether populations are locally adapted, reciprocal transplantations of populations among their respective sites of origin are required (Kawecki & Ebert 2004). If genetic differentiation among populations represents local adaptation, the local populations should outperform non-local populations. To investigate whether evidence of local adaptation could be detected, I performed reciprocal transplants among four natural populations of P. farinosa. The experiment revealed some effects of population of origin on plant performance across transplant sites, further indicating that populations are genetically differentiated. However, no evidence of local adaptation was found. Moreover, large site effects were found for all fitness components examined, indicating considerable phenotypic plasticity (paper IV).

Lack of local adaptation to current conditions may result from temporal variation in selection, low genetic diversity and high levels of gene flow (Bradshaw 1965; Linhart & Grant 1996; Kawecki & Ebert 2004; Leimu & Fischer 2008). According to theory, genetic differentiation in response to spatial heterogeneity is more likely to occur in response to large variation in the selective environmental variables and the magnitude of adaptive differentiation depends on the level of gene flow among populations (Via & Lande 1985; Van Tienderen 1991; Kawecki & Ebert 2004). Moreover, adaptive genetic differentiation is likely to occur in response to consistent differences in the direction of selection, whereas phenotypic plasticity should be favored if variation in environmental conditions is short-term and predictable (e.g., Bradshaw 1965; Alpert & Simms 2002).

Our results indicate that selective factors associated with vegetation height have contributed to genetic population divergence in reproductive effort. These factors may include both intensity of competition for light and nutrients, and conditions for seedling establishment. The fact that substantial differences in several fitness components were documented among populations of origin suggests that the populations are genetically differentiated. However, the results of the reciprocal transplant experiment did not reveal any evidence of local adaptation to current environmental conditions. In perennial plants, fitness differences between populations of origin transplanted to a common site may develop only over considerable time (Bennington et al. 2012). The great Alvar has a long history of grazing by cattle, sheep and horses, but the intensity of grazing and clearing of wood in the area has varied considerably over the past centuries (Ekstam
The observed genetic differentiation may thus represent the response to selection over a relatively long period of time, and the lack of evidence for local adaptation may be associated with relatively large changes in land use over the last decades.

Concluding remarks

Taken together, the results of this thesis suggest that the evolution of plant reproductive traits and plant life histories are closely linked, and that the nature of the relationship between reproductive traits and life history trade-offs, such as the cost of reproduction, varies among environments (paper I). The results further show that environmental context influences how biotic interactions affect population dynamics, and that a given environmental factor can influence population growth rate in different directions through direct effects on potential population growth rate and indirectly via effects on intensity of biotic interactions and on the sensitivity of population growth rate to these biotic interactions (paper II). Our results further suggest that variation in reproductive effort observed among populations in the field is a function of both genetic differences and plastic responses, and that both genetic differentiation among populations and plastic responses are associated with environmental heterogeneity (paper III). Still, there was no evidence of that such genetic population differentiation represent local adaptation to current habitat conditions in reciprocal transplant experiments among four populations (paper IV). Moreover, differences in performance among populations of origin were small compared to effects of transplant site, suggesting that differences in reproductive strategies among natural populations largely result from plastic responses to local habitat conditions.

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Svensk sammanfattning

Miljövariation, populationsdynamik och livshistoriedifferentiering hos *Primula farinosa*

Den här avhandlingen handlar om hur populationsdynamik och reproduktionsstrategier hos växtpopulationer påverkas av rumslig variation i abiotiska och biotiska miljöförhållanden. Växters populationstillväxt bestäms av individernas tillväxt, överlevnad och reproduktion. Variation i populationstillväxt har tidigare kopplats till variation i jordens sammansättning av näringsämnen, markanvändning och markfuktighet samt till variation i den biotiska miljön, t ex i form av interaktioner med pollinatörer, fröpredatorer och omgivande vegetation. Dessa interaktioner kan i sin tur påverkas av lokala miljöförhållanden. Dels kan förekomst och abundans av fröpredatorer och pollinatörer variera med rumslig miljövariation, dels kan effekten av reducerad fröproduktion på värdväxtens populationstillväxt variera med den omgivande miljön.

Olika miljöförhållanden kan även ha stor inverkan på växters resurstillgång och individers fördelning av resurser mellan tillväxt och reproduktion. Förutsatt att en individs resurstillgång är begränsad sker tilldelning av resurser till reproduktion på bekostnad av tillväxt. Hos fleråriga växter kan en hög satsning på reproduktion leda till hög reproduktiv framgång, men också till kostnader i form av lägre vegetativ tillväxt, överlevnad och framtda reproduktion. Dessa reproduktiva kostnader är ofta mer uttalade i miljöer där tillgången på resurser är låg. I miljöer med god resurstillgång kan många växter kompensera för den ökade kostnaden reproduktionen innebär med ökat upptag av resurser och därmed hålla den negativa effekten av reproduktion på en låg nivå.

Skillnader i reproduktiv kostnad mellan olika miljöer kan påverka den optimala *reproducitiva ansträngningen*, dvs. fördelningen av resurser mellan tillväxt och reproduktion. I miljöer där reproduktiva kostnader för växter är låga kan det långsiktigt vara fördelaktigt med hög reproduktiv ansträngning, medan lägre reproduktiv ansträngning kan vara fördelaktig om kostnaderna för reproduktion är höga. Även skillnader i överlevnad mellan populationer kan påverka den optimala fördelningen av resurser. I miljöer där chansen att överleva ökar med ökad plantstortlek kan organiser dra fördel av att snabbt växa sig stora och alltså satsa på tillväxt på bekostnad av överlevnad. Storleksberoende mortalitet återfinns ofta i stabila miljöer, där konkurrensen om växtplatser, näring, ljus etc. ofta är hög. Tidig hög reproduktiv ansträngning, på bekostnad av tillväxt, kan däremot vara fördelaktigt i miljöer där dödligheten är hög och oförutsägbar, såsom i områden som ofta drabbas av bränder, torka eller översvämningar. Betande djur kan också bidra till hög och oförutsägbar mortalitet till följd av klövtramp och andra skador till följd av bete.

Om miljörelaterade selektionstryck består under lång tid kan detta leda till *genetisk differentiering*, dvs. genetiska anpassningar till den lokala miljön, i reproduktiv ansträngning mellan växtpopulationer. Huruvida genetisk differentiering faktiskt sker beror på graden av miljövariation, den rumsliga skalan för variationen, på mängden genutbyte mellan populationer och genetisk diversitet. Genetisk differentiering är också mer sannolik om förändringar i miljön består under långa tidsperioder, medan *fenotypisk plasticitet*, dvs. morfologiska anpassningar till den lokala miljön, kan gynnas om förändringarna sker på kortare tidsskalor och om dessa


För att undersöka huruvida kostnader för reproduktion, i form av negativa effekter på framtida tillväxt, reproduktion och överlevnad, kunde knytas till variation i vattentillgång och blomkarakterer, förhindrades reproduction hos ett antal uppmärkta individer. Detta gjordes genom att avlägsna knoppar och blommor i början av blomningssäsongen på åtta lokaler av varierande markfuktighet och på både långstjälkade och kortstjälkade individer. Kostnad för reproduction mättes i form av tillväxt och blomproduktion följande växtsäsong hos manipulerade individer jämfört med hos icke-manipulerade individer. Resultaten visade att kostnader för reproduktion varierade mellan populationer och var högre hos lång-stjälkade individer. Variation i kostnad för reproduktion kunde kopplas till skillnader i jordfuktighet. Kostnader uppmättes vid låg respektive hög vattentillgång. Variation i reproduktiv kostnad mellan olika miljöer skulle på lång sikt kunna leda till genetisk differentiering mellan populationer i reproduktiva strategier.

Den andra studien behandlade variation i populationstillväxt, fröpredation och känslighet för fröpredation till följd av rumslig miljövariation. I denna studie jämfördes potentiell populationstillväxt, dvs. populationstillväxt beräknad på total fruktfördoproduktion (inklusive angripna frukter) med realiserad populationstillväxt, dvs. populationstillväxt baserad på realiserad fruktfördoproduktion (icke angripna frukter). På så vis var det möjligt att uppskatta hur stor inverkan
fröpredationen hade på populationstillväxt på olika lokaler. Resultaten visade att populationstillväxten påverkades både av graden av fröpredation och av populationstillväxternas känslighet för förändringar i fröproduktion. Dessutom visade det sig att samma miljövariabel, markfuktighet, hade både positiva och negativa effekter på populationstillväxt. Resultaten av denna studie visar att effekten av biotiska interaktioner på populationstillväxt påverkas av variation i miljöfaktorer som markfuktighet och vegetationshöjd, både direkt, via effekter på potentiell populationstillväxt, och indirekt, via effekter på predationsintensitet och populationers känslighet för förändringar i fröproduktion, och att realiserad populationstillväxt inte alltid speglar förhållandet mellan fröpredatorer och deras värdväxter.

För att ta reda på om miljörelaterad variation har resulterat i genetisk differentiering i reproduktiv ansträngning mellan populationer genomfördes ett experiment där från 20 naturliga Alvar-populationer samlades in och kultiverades i en experimentell trädgård vid Stockholms universitet. I ursprungspopulationerna var den reproduktiva ansträngningen högre hos populationer som växte i kort vegetation än hos populationer som växte i hög vegetation. Reproduktiv ansträngning var också högre i torra miljöer. De experimentella populationerna i trädgårdsexperimentet uppvänsade också viss variation i reproduktiv ansträngning, vilket tyder på att den variation i reproduktiv ansträngning som observerats i fält delvis representerar genetisk differentiering mellan populationer. Dessutom var reproduktiv ansträngning i trädgårdsexperimentet också kopplad till vegetationshöjd i ursprungspopulationerna. I likhet med ursprungspopulationerna var reproduktiv ansträngning högre hos individer som härstammade från populationer med kort vegetation. Däremot fanns inget samband mellan reproduktiv ansträngning hos de experimentella populationerna och markfuktighet i ursprungslokalerna, vilket tyder på att sambandet mellan markfuktighet och reproduktiv ansträngning i fält representerar fenotypisk plasticitet.

För att undersöka om den genetiska variationen som dokumenterades i trädgårdsexperimentet representerade lokal anpassning till rådande miljöförhållanden utfördes ett transplantationsexperiment mellan fyra populationer av varierande jorddjup, markfuktighet och vegetationshöjd. Även detta experiment gav vissa indikationer på att det förekommer genetiska skillnader mellan populationerna. Däremot fanns inga tecken på lokal anpassning. En förklaring till detta kan vara att de skillnader som observeras idag kan vara anpassningar till tidigare miljöförhållanden. Dessutom var effekten av transplantationslokal stor, vilket tyder på att en stor del av den variation som observeras i fält beror på fenotypisk plasticitet i respons till den dokumenterade variationen i miljöförhållanden. Den relativa framgången hos de olika ursprungspopulationerna skilde sig beroende på vilken fitness-komponent som undersöktes, vilket belyser problematiken med att studera enskilda fitness-komponenter vid studier av lokal anpassning.

Sammanfattningsvis tyder resultaten av dessa studier på att evolutionen av reproduktiva karaktärer och livshistoriemönster är tätt sammankopplade, men att deras förhållande sinsemellan varierar mellan olika miljöer. Dessutom påverkar den lokala miljön hur biotiska interaktioner påverkar populationstillväxten, och en given miljövariabel kan påverka populationstillväxt i olika riktningar via effekter på potentiell populationstillväxt, styrkan av biotiska interaktioner, och hur känslig populationstillväxten är för biotiska interaktioner. Resultaten antyder också att variation i reproduktiv ansträngning mellan populationer i fält är resultatet av både genetiska skillnader och plastiska responser. Däremot kan denna differentiering inte kopplas till rådande miljöförhållanden.
Tack!


Tove