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Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*

Thesis for the degree of Philosophiae Doctor

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Mohsen Falahati-Anbaran

Contents

List of papers

This thesis is based on four papers.

I) Lundemo S, Falahati-Anbaran M, Stenøien HK (2009) Seed banks cause elevated generation times and effective population sizes of *Arabidopsis thaliana* in northern Europe. *Molecular Ecology* 18, 2798-2811.

II) Falahati-Anbaran M, Lundemo S, Ågren J, Stenøien HK (2011) Genetic consequences of seed banks in the perennial herb *Arabidopsis lyrata* subsp. *petraea* (Brassicaceae). *American Journal of Botany* 98(9): 1475–1485.

III) Falahati-Anbaran M, Lundemo S, Stenøien HK. Quantifying dispersal in time and space in northern European populations of *Arabidopsis thaliana* (manuscript).

IV) Falahati-Anbaran M, Lundemo S, Ansell SW, Stenøien HK. Contrasting patterns of genetic structuring in natural populations of *Arabidopsis lyrata* subsp. *petraea* across heterogeneous regions in Northern Europe (manuscript).

Declaration of contribution

In paper I, HKS initiated the project and organized, HKS and SL did the field work, HKS, SL and MFA performed the analysis and all authors contributed to write the paper. The project in paper II was initiated by HKS, SL did the field work, HKS, SL and MFA did the data analysis, MFA and SL wrote the paper with contribution from the other authors. In paper III, HKS initiated the experiments. HKS, MFA and SL designed and conducted the field work; MFA analysed the data and wrote the paper with the contribution from the other authors. In paper IV, HKS, SL and MFA initiated the project, MFA and SL planned and conducted the field work, MFA, SL analysed the data, MFA wrote the paper with contribution from the other authors.

Summary

In most plant species, seeds after dispersing from the mother plant (primary dispersal) may undergo secondary dispersal, either in time by remaining dormant in the soil and forming a seed bank, or in space by movement to other locations. Seed bank and dispersal in space are bet-hedging strategies that minimize the extinction risk and aid to population stability and persistence in temporally variable environments. The ability to establish seed bank via depositing a fraction of seeds into the soil may also increase the potential of early stage adaptation into new habitats. A persistent seed bank preserves genetic diversity and buffers populations from the loss of genetic variants due to random drift. Although theoretical studies have highlighted the role of seed banks in elevating effective population size, little information exists regarding the evolutionary potential of seed banks in natural populations.

In this thesis I studied inter- and intraspecific variation in genetic composition of seed banks and its significance in natural populations of two closely related species in the genus *Arabidopsis*. *A. thaliana* is an annual self-compatible plant whereas *A. lyrata* is perennial and self-incompatible. The potential contribution of seed banks to effective population size (N_e), generation time, genetic variation, and population dynamics has been addressed. The pattern of dispersal over time and space was investigated by monitoring of natural populations over five consecutive years in *A. thaliana*. In addition, regional differences in seed bank, genetic composition and structure in *A. lyrata* were investigated between three contrasting regions in northern Europe.

The results showed that both species form persistent seed banks throughout their Norwegian distribution range. Seedling density was lower in *A. lyrata* than *A. thaliana*, as would be expected from a perennial. Moreover, the seed bank contributes to total effective population size in perennial *A. lyrata*, though not to the same extent as in *A. thaliana*. In *A. lyrata* both seed bank and above-ground individuals seemingly have a similar contribution to the total N_e.

Monitoring *A. thaliana* populations over multiple years revealed that in most populations two or more distinct multilocus genotypes were present, which often varied in frequency between years, leading to variation in within-population diversity. Although most of the distinct multilocus genotypes within each population were genetically similar, probably due to historical mutation and recombination events, in some cases multiple colonization events due

to migration from other populations were evident. Many geographically closely situated populations shared common multilocus genotypes and expressed low differentiation compared to distant ones. The results show evidence dispersal in time, i.e., persistence of dormant or ungerminated seeds in ten populations in which 29% of seeds descended two or three years before present, on average. Additionally there are signs of seed and pollen immigration from other populations in almost one fifth of the studied cohorts, reflecting an effective migration rate of 1.8% per generation. Migration through pollen and seeds in *A. thaliana* is therefore common, and the seed bank plays, at the same time a substantial role in overall population dynamics.

Comparing natural populations of *A. lyrata* in different regions revealed that soil seed banks are either absent or small in Icelandic populations and average density of seed bank is 2.5 fold smaller than what was observed among Norwegian populations, though the overall differences between regions was not statistically significant. The level of genetic variation in Icelandic was similar to Swedish and significantly higher than what found in Norwegian populations. In addition population differentiation on Icelandic was significantly lower than what found in Swedish and Norwegian populations. When comparing similar distribution areas in the regions, the effect of habitat structure was found to be less important to explain the differences in genetic structuring. Immigration rate over time was similar between regions that show variable population differentiations. The results suggest that relatively low differentiation among Icelandic populations is more likely due to large historical effective population sizes compared to Scandinavian populations, rather than immigration *per se*.

Introduction

Seeds and seed related traits

Seed size, the establishment of seed banks and dispersal in space are important traits that may influence population persistence, the colonization and extinction time and interact with environmental variables (Cohen 1966; Silvertown 1981; Brown & Venable 1986; Venable & Brown 1988; Guo *et al.* 2000). In most flowering plants seeds after dispersing from the mother plant (primary dispersal), may experience dispersal events, either by remaining dormant in the soil (seed bank formation), or in space by movement to other locations (dispersal in space). Seed bank formation and seed dispersal are bet-hedging strategies which enable plants to escape unfavorable environmental conditions (Venable & Brown 1988). Seed size is highly variable and may vary over ten orders of magnitude among species, from dust-like seeds of orchids being as small as 0.3µg to the 20 kg seeds of the double coconut (Arditti 1967; Harper *et al.* 1970; Silvertown 1981; Moles *et al.* 2005; Linkies *et al.* 2010). Although large seed size has been attributed to higher survival rate, there is a tradeoff between seed size and seed number (Jakobsson & Eriksson 2000). A negative relationship has been observed between seed size and number for many species across different habitat types (Jakobsson & Eriksson 2000; Metz *et al.* 2010). Although large seeds generally have a higher chance to establish, they may experience higher mortality due to higher predation rate. In addition, a tradeoff exists between seed size and dispersal ability in which larger seeds may have limited possibilities for long distance dispersal (e.g., Parciak 2002). Generally speaking, small seeds are more easily dispersed and may thus facilitate colonization into new environments (e.g., Silvertown 1981).

Ecology of seed banks

A seed bank is a deposit of viable and ungerminated propagules, and can exist both as mature seeds on the plant (aerial seed bank) or in the soil (soil seed bank), whereas in animals this trait is evident through diapausing eggs (Cohen 1966; De Stasio 1990; Christoffoleti & Caetano 1998). Delayed germination of seeds is a bet-hedging strategy to minimize the risks of germinating at the wrong time of the growth season, and in face of unpredictable environmental disturbances (Cohen 1966; Childs *et al.* 2010). Bet-hedging has been widely investigated theoretically and empirically (e.g., Venable 2007 and references therein). While

fluctuations in environmental conditions may increase the rate of mortality and variance in reproductive success among years, seed banks may have substantial potential in buffering variation in reproductive success and minimize the extinction risk (Pake & Venable 1996).

Seeds can either persist in the soil for a short time until the next germination season (less than a year; transient seed bank) or remain in the soil as dormant beyond one year (persistent seed bank; Thompson & Grime 1979). The existence of seed banks in plants in terrestrial and aquatic ecosystems has been well documented (Thompson & Grime 1979; Leck *et al.* 1989; Thompson *et al.* 1997; Evans *et al.* 2007), and although seed dormancy has been strongly attributed to formation of seed bank, empirical studies have found no close relationship between dormancy and seed bank formation (Thompson *et al.* 2003; Honda 2008). Perennial and large seed species are less capable to establish seed banks than annual and small seed species (Silvertown 1981; Thompson 1987; Honda 2008), and large seeds usually less able to persist for longer periods of time in the soil (Thompson 1987). The number of seeds found in the seed bank of annual and biannual plants is often higher than in perennials, indicating the greater capacity of annual species to persist in the soil seed bank than perennials (Arroyo *et al.* 2006; Honda 2008; DeFalco *et al.* 2009). Seeds of plant species may remain in soil as dormant or ungerminated for a few years up to several decades, centuries, or even >1000 years (Kivilaan & Bandurski 1981; Shen-Miller *et al.* 1995; Thompson *et al.* 1997; Telewski & Zeevaart 2002). Although the ecological potential of seed traits has been extensively studied in numerous species (Howe & Smallwood 1982; Thompson 1987; Bakker 1996), little information exists about the evolutionary importance of secondary seed dispersal over time (seed bank) and space (migration) in plants that differ in several life history traits.

Seed banks and effective population size

Most annual species and some perennials maintain seed banks, and the seed bank will over time contain seeds of different genotypes as not all seeds germinate directly after reproductive events. This buffering effect can dampen the rate of loss of genetic variation due to stochastic variation in the environment and increase the effective population size (Templeton & Levin 1979; Hairston & De Stasio 1988). Genetic variation in plant populations harbouring seed banks is influenced by mutual gene flow between the seed-bank and the above-ground individuals. Theoretical expectations and experimental studies suggest that seed banks may moderate the effect of genetic drift through buffering against changes in census sizes in

above-ground cohorts (Epling *et al.* 1960; Templeton & Levin 1979; Nunney 2002; Vitalis *et al.* 2004; Honnay *et al.* 2008). Estimations of effective population size should therefore be based on both seeds from the seed-bank and above-ground individuals.

The effective size of a given population (N_e) can be defined as the size of an ideal population that looses genetic variation (through genetic drift) between generations at the same rate as the natural population under study (Wright 1931; Kimura & Crow 1963). Estimation of effective population size from genetic and ecological data is a challenging topic in evolutionary biology and many different methods have been proposed, though most of them are based on simplified assumptions that seldom apply to real populations (for review see: Leberg 2005; Wang 2005). These approaches, which can be used to estimate contemporary and historical N_e, are based on both demographic and genetic models (Schwartz *et al.* 1999; Nunney 2002; Leberg 2005; Wang 2005). Genetic models based on heterozygosity excess (Pudovkin *et al.* 1996), temporal shifts in allele frequency (Krimbas & Tsakas 1971; Waples 1989; Wang 2001) and linkage disequilibrium, LD (Hill 1981; Waples 1991; Waples & Do 2008, 2010) have received considerable attention in the estimation of N_e (Luikart *et al.* 2010). The LD method offers an unbiased single sample estimator of contemporary N_e (Bartley *et al.* 1992; Waples & Do 2008), and has been shown to perform better than the temporal method (Waples & Do, 2010) as it needs only a single time point per population, whereas the latter require data from at least two time points for each population. Coalescent theory may also be used to infer the demographic history of populations through estimating historical N_e based on ancestral relationships among individuals (Fu & Li 1999). Historical N_e infers the amount of genetic diversity over evolutionary time since formation of a population, reflecting bottlenecks, range expansions, migration and admixture events in the past. Neutral genetic diversity within populations is positively related to the coalescence time and effective population size.

Gene flow through seed and pollen dispersal

In flowering plants, dispersal is the movement of genes through seeds or pollen from one site to another (Endler 1977; Levin 1981). If a given dispersal event results in establishment or reproduction within the local gene pool, gene flow has occurred (Endler 1977). Gene flow among populations may increase within-population genetic diversity and reduces genetic differentiation between local populations (Ehrlich & Raven 1969). Type of mating system

play an important role in determining the level of gene flow through pollen dispersal, in which in an outcrossing plant exhibiting a self-incompatibility (SI) system, a higher level of gene flow is often expected between populations in a given space compared with predominantly self-pollinating species because the former is highly dependent on pollen flow from other individuals of the same species (e.g., Govindaraju 1988a,b; Mable & Adam 2007). The SI system in plants prevents fertilization by self-pollen and accepts only pollen from genetically unrelated individuals, thus facilitating outcrossing. Seed dispersal in plants is often expected to be a distance dependent process, i.e. with higher seed movement over short distances compare to long distances (Howe and Smallwood 1982 and references therein). However, long distance seed dispersal is very important because it can affect on colonization processes and metapopulation dynamics (Cain *et al.* 2000).

Molecular techniques have been used extensively to study the pattern of pollen and seed dispersal (Ouborg *et al.* 1999). Dispersal can be quantified using direct (parentage analysis and assignment test) and indirect approaches using population structure (e.g., genetic differentiation measures like F_{ST}; Slatkin 1987; Cain *et al.* 2000). Historical gene flow patterns has traditionally been studied using a simple population structure model introduced by Wright (1931), in which the relationship between the number of immigrants a population receive and population differentiation (F_{ST}) can be shown as $F_{ST} = [1/(1+4Nem)]$, where N_e and m is the effective population size and migration rate per generation, respectively. However, this model is based on a large number of simplifying assumptions that are unlikely to hold true for natural populations (Whitlock & McCauley 1999). In addition, this method is not appropriate to study the spatial patterns of genetic structure and gene flow among subpopulations (Hutchison & Templeton 1999; Sork *et al.* 1999).

The pattern of gene flow among populations in a given geographical area is often quantified through isolation by distance, IBD. Under a stepping-stone model of population structure, the relative influence of gene flow and genetic drift on regional population structure can be inferred from the relationship between genetic and geographic distance among pairs of populations (Kimura & Weiss 1964). The pattern of IBD can thus be compared between regions to determine how gene flow and drift have contributed in shaping the genetic composition within a given region compared with others. In this model, gene flow is expected to decline with increasing geographic distance between populations. In species with restricted seed and pollen dispersal between populations, a significant relationship is expected between

genetic and geographic distance, leading to isolation by distance (Slatkin 1993). Several factors may affect the pattern of IBD, such as the scale and regional topography in which populations are being sampled, number of populations, and time since colonization of a locality (Crispo & Hendry 2005). The absence of IBD has been attributed to several factors such as recent colonization of regions followed by rapid range expansion or fragmentation (Slatkin 1993; Hutchison & Templeton 1999; Crispo & Hendry 2005).

Aims of the study

In this thesis I have used two closely related species, both of which are widely used as models in research, to study the ecological and evolutionary importance of seed banks and dispersal. In particular, I have tried to discern how annual and perennial species differ in their strategies for dealing with environmental stochasticity, and more specifically, whether the importance of seed banks differ in annual and perennial plants.

The main objectives addressed in this thesis are:

1) To investigate the existence of seed banks in *A. thaliana* and *A. lyrata* and to determine the relative contribution of the seed bank to total effective population size and generation time (Papers I and II)

2) To study the pattern of secondary seed dispersal in time and space by quantifying the effective seed and pollen migration rate and dispersal in time in *A. thaliana* (Paper III)

3) To study the pattern of genetic diversity and structuring in *A. lyrata* inhabiting contrasting habitats (Paper IV)

Materials and methods

Study species

Arabidopsis thaliana (L.) Heynh. (Figure 1), known as mouse-ear cress or wild thale cress, is a weedy annual, self-pollinating plant in the mustard family (Brassicaceae). The plant has small, white flowers, and can produce large amounts of small seeds (~0.1-0.5 mm long, Figure 2). In Scandinavia it predominantly germinates in the autumn, overwinters as a rosette and does flower and sets seed in early spring. It is diploid (2n = 10) with a relatively small genome, 125Mb, and has been extensively used as a model for molecular biology and ecological and evolutionary studies (Mitchell-Olds & Schmitt 2006; Koornneef & Meinke 2010). The plant is native to Eurasia and North Africa (O'Kane & Al-Shehbaz 1997; Al-Shehbaz & O'Kane 2002). Additionally, the species has been introduced and successfully established in central and Northern Europe, North America, southwest Asia, Australia and New Zealand (Sharbel *et al.* 2000; Al-Shehbaz & O'Kane 2002; Hoffmann 2002).

Figure 1: Floral display in *Arabidopsis thaliana* (right) and *A. lyrata* (left). Photo: M. Falahati-Anbaran.

In Norway *A. thaliana* occurs in wide range of habitats from sea level and up to 1150 m asl and distributed from 58°N to 69°N. The plant occupies mainly disturbed areas such as road verges, railway tracks, and rocky slopes with thin soil layer and low vegetation cover (Figure 3).

Figure 2: Variation in flower and seed size between *Arabidopsis thaliana* (right) and *A. lyrata* (left). Photo: M. Falahati-Anbaran

Arabidopsis lyrata subsp. *petreae* (L.) O'Kane & Al-Shehbaz (1997), northern rock cress, is a perennial and self-incompatible herb that is distributed over disjunctive regions in Central and Northern Europe (Jonsell *et al.* 1995). *A. lyrata* is closely related to *A. thaliana*, and it is believed they diverged from a common ancestor about 5-10 million years ago (Koch *et al.* 2000; Hu *et al.* 2011). In contrast to *A. thaliana*, *A. lyrata* has larger flowers (Figure 1) and seeds (1-1.5 mm long, Figure 2). It is diploid (2n = 16) with a larger genome (207 Mb, Hu *et al.* 2011) than *A. thaliana*, and has been extensively used as a model in ecological and evolutionary studies (Mitchell-Olds 2001). In northern Europe, the plant is restricted to mountainous areas of south-western Norway, a small part of the eastern coast of Sweden, United Kingdom, Faeroe Islands and across most of Iceland (Jonsell *et al.* 1995; Schmickl *et al.* 2010). In Norway, the plant grows in habitats located from the sea level up to ~ 1700 m asl and deep valleys and mountain peaks my thus create physical barriers limiting connectivity between populations (Figure 3). In contrast, *A. lyrata* in Sweden occur mostly in open habitats

along the coast, with no major physical barriers between sites. In Iceland the plant is found on lava plain and disturbed and open habitats from see level to highlands.

Figure 3: Typical habitat of *Arabidopsis thaliana* locality at Byneset, Trondheim (top), and *A. lyrata* locality in Sæbo, Eidfjord (bottom). Photo: M. Falahati-Anbaran.

Seed and soil samples

Seeds from above-ground plants were sampled from natural populations of *A. thaliana* across its Norwegian distribution range between 2005 and 2009 (Papers I and III). Soil samples (ten samples in each population; ~10 × 10 cm, 1-5 cm deep) were randomly collected throughout each population before seed dispersal in late May and early June 2005, 2008 and 2009 (Papers I and III).

In *A. lyrata*, soil samples were collected from 14 populations in southwestern Norway, in which the above-ground individuals were previously analysed by Gaudeul *et al.* (2007), (Paper II) in July 2006, before that year's seed rain. Soil and rosette leaves from ten Icelandic populations of *A. lyrata* were sampled in 2009 (Paper IV).

A. thaliana seeds were sown in the greenhouse and leaf tissue was collected from one individual per maternal plant (Papers I and III). Soil samples were stored at 4 ºC before germination trials to break dormancy of seeds. Thereafter, the soil was spread out in a thin layer on top of commercial potting soil in 12.8 × 14.5 cm pots to stimulate germination of seeds (Papers I, II, III and IV). Pots were placed in the greenhouse under 16 h day length for about 10 months until no more seedlings emerged. The temperature and humidity during the germination experiment were 20 °C and 65%, respectively. Leaf tissue from each emerged seedling was collected separately. The leaves obtained from above-ground individuals and seedlings emerging from the soil samples were dried at 45 °C for 24 h (Papers I, II, III and IV).

Molecular and data analyses

Genomic DNA was extracted from individual plants of above-ground and seed-bank cohorts using the E.Z.N.A. ™ SP Plant DNA Kit (Omega Bio-Tek, Inc). *A. thaliana* samples were screened using 107 (Paper I) and 103 (Paper III) SNP markers described in Törjék *et al.* (2003). Eleven (Paper I) and twenty one (Paper III) SNPs were excluded with no call or low efficiency after genotyping. *A. lyrata* samples were screened with 15 (Paper II) and 21 (Paper IV) microsatellite markers. The primer sequences of flanking regions for microsatellite loci used in *A. lyrata* are described in Bell and Ecker (1994), Clauss *et al.* (2002), Loudet *et al.* (2002), and Kuittinen *et al.* (2004).

Seed bank density between species was compared using a Mann-Whitney *U* test (Paper II). The within-species variation between contrasting habitats was investigated by comparing density of seed bank in Icelandic *A. lyrata* to that in Norwegian populations (Paper IV). Population genetic parameters and pairwise F_{ST} (Weir & Cockerham 1984) were estimated using Arlequin 3.5 (Excoffier *et al.* 2005), FSTAT (Goudet 1995) and Genepop (Rousset 2008; Papers I, II, III and IV). Analysis of molecular variance, AMOVA, was conducted using Arlequin (Paper I). Genetic structure was also inferred by model based Bayesian methods as implemented in Structure (Pritchard *et al.* 2000; Falush *et al.* 2003; Papers I, II and IV), BAPS (Corander & Marttinen 2006; Corander *et al.* 2008; Papers I and II) and Instruct (Gao *et al.* 2007; Paper III). The results of Bayesian analyses were summarized across multiple runs using CLUMPP (Jakobsson & Rosenberg 2007). Spatial structure was investigated using isolation by distance (IBD). IBD was performed by regressing genetic distance against geographical distance and the significant was tested by permutation test using GeneAlex (Peakall & Smouse 2006; Papers I and IV). Contemporary N_e was estimated with a linkage disequilibrium approach implemented in NeEstimator 1.3 (Peel *et al.* 2004; Paper II). Historical effective population size (N_e) was estimated based on a coalescent-based maximum likelihood method implemented in Migrate (Beerli & Felsenstein 1999, 2001; Papers I, II and IV). Dispersal in space was quantified by a conservative estimate based on distance criterion using an assignment test (Cornuet *et al.* 1999). Migration through pollen dispersal was also computed by identifying individuals carrying two or more private alleles at heterozygous SNP loci in each cohort. The effective migration rate, i.e. dispersal and establishment, was calculated combining both seed and pollen flow events for each population. Dispersal in time was estimated by assigning above-ground individuals sampled in 2009 to the previous above-ground cohorts using a distance based criterion (Nei *et al.* 1983) implemented in GeneClass2 (Piry *et al.* 2004). Analysis of variance, ANOVA, was conducted to test for differences between regions for various parameters (Iceland, Norway and Sweden) and the difference between regions was examined using a post hoc Bonferroni test (Paper IV). A Welch F test was used to examine differences in population differentiation (pairwise F_{ST}) among regions and multiple comparisons was conducted using Tamhane's test (Paper IV). Analysis of covariance, ANCOVA, was used to test the regression slope of isolation by distance between regions (Paper IV). All statistical analyses were performed using SPSS version 16.

Results and discussion

Seed banks in A. thaliana and A. lyrata (Papers I and II)

The results revealed that both species maintained persistent seed banks in their northern European distribution range. The seed bank density as determined by the germination method varied considerably within *A. thaliana* and *A. lyrata* populations. Overall, the seedling density in *A. thaliana* was an order of magnitude higher than in *A. lyrata*. Because soil samples were collected before seed rain, any evidence of germination from soil samples indicates the presence of a persistent seed bank. Seed banks were detected in all *A. thaliana* populations in 2005. In contrast, in 2 out of 14 *A. lyrata* Norwegian populations, no seedlings were detected. The results may indicate that the existence of a persistent seed bank is more important for annual plants than for perennials. The discrepancy in seedling density between the study species can mainly be attributed to differences in life history traits, which is in agreement with theoretical predictions and empirical studies, showing that annual plants in general have higher reproductive output than perennials (Harper & Ogden 1970; Hirshfield & Tinkle 1975; Primack 1979). Moreover seed size in *A. thaliana* a priori is considerably smaller than *A. lyrata* and it has been shown that large seed species may capable less to persist in the soil for long time relative to small seed ones (Silvertown 1981; Thompson 1987). The results are in agreement with previous studies showing a higher seed bank density in annual than perennial species (e.g., Arroyo *et al.* 2006). Although the seed bank density in Icelandic populations of *A. lyrata* was 2.5 fold smaller than that in Norwegian populations, the difference was not statistically significant ($P = 0.088$). Most Icelandic *A. lyrata* populations either lacked completely a seed bank (30%) or had low seedling densities (60%; < 50 viable seeds pr m^{-2}) and in only one population the density of seed bank was high (10%; > 100 viable seeds pr m^{-2}). The results also showed no differences between population densities (rosettes per m^{-2}) between regions. Variation in seed production between regions may be attributed the differences in seed production rather than population density (Vergeer & Kunin 2011). Other ecological and biological factors such as soil particle size, soil nutrient levels, and microbial activities may also influence the density of seeds in the seed bank (Wagner & Mitschunas 2008; DeFalco *et al.* 2009)

Genetic diversity and structure (Papers I and II)

The level of genetic diversity did not vary between seed bank and above-ground cohorts in either *A. thaliana* or *A. lyrata*, suggesting that most genetic variability in the seed bank is present in above-ground cohorts. This has also been reported in other studies, both for annual and perennial species (Mahy *et al.* 1999; Mandák *et al.* 2006). The average between-cohort differentiation, i.e. between seed bank and above-ground plants, was considerably lower than that among populations for both *A. thaliana* and *A. lyrata.* Similarly, model based Bayesian clustering revealed a high level of structure in Norwegian populations of *A. lyrata* and *A. thaliana.* In *A. thaliana*, populations were assigned to 15 ancestral clusters based on seed-bank (2005 samples) and above-ground (2005 and 2006) data. In most populations the seed-bank and above-ground cohorts were genetically similar. A significant correlation was detected between genetic and geographical distance in Norwegian populations of *A. thaliana*, indicating isolation by distance pattern for all cohorts. This suggests a high level of gene flow relative to drift over short geographical distance, and relatively lower gene flow relative to genetic drift at longer distance (Hutchison & Templeton 1999). In *A. lyrata*, Bayesian clustering based on seed bank and above-ground data revealed a high level of structure among populations and most of seed bank and above-ground cohorts for each population were grouped to similar ancestral clusters.

Evolutionary consequences of seed banks (Papers I and II)

The contribution of the seed bank to total effective population size (N_e) was quantified by estimating the scaled mutation parameter (θ) for individual seed-bank (θ_S) and above-ground 2005 ($\theta_{A\text{-}5}$) and combined (θ_T) cohorts using SNP data in *A. thaliana*. The results showed that the total N_e, i.e. when combining seed-bank and above-ground individuals, was greater than when considering the above-ground cohort alone. A similar result was observed based on estimates of historical and contemporary effective population size in *A. lyrata*. Interestingly, the relative ratio measured by θ_T/θ_A was higher in *A. thaliana* than *A. lyrata*, suggesting a weaker contribution of the seed bank to N_e in the later species. In *A. lyrata,* θ_S/θ_T was slightly lower than θ_A/θ_T, but not statistically significant, suggesting a similar contribution of both seed-bank and above-ground cohorts to total N_e. Although the historical effective N_e based on the coalescence method was significantly higher than contemporary N_e estimates, a similar relative ratio was obtained based on both methods for *A. lyrata.* Generation time in *A. thaliana* was estimated based on the model introduced by Vitalis *et al.* (2004). This was

conducted by estimating the total effective population size from a subset of populations using microsatellite data obtained from Stenøien *et al.* (2005). Thus, generation time in Norwegian populations of *A. thaliana* was found to be on average 4 years (range 1-8), and only two out of six (33%) populations showed a generation time of one year. This is a rough estimate of generation time in natural populations of plant species based on molecular data. This indicate that presence of seed bank elevate generation time by differential recruitment of seeds of different genotypes preserved in the soil. Taken together these results support theoretical expectations, that seed banks can substantially increase the total N_e in both annual and perennial species (Hairston & De Stasio 1988; Kaj *et al.* 2001; Nunney 2002; Vitalis *et al.* 2004; Waples 2006).

Pattern of dispersal in time and space in A. thaliana (Paper III)

A. thaliana can spread rapidly into new areas (Jørgensen & Mauricio 2004) and it has been suggested that local populations experience extensive metapopulation dynamics with occasional extinctions and subsequent recolonization by immigrations from other populations (Bergelson *et al.* 1998; Lavigne *et al.* 2001; Le Corre 2005). Both dispersal in space (immigration from other populations) and dispersal in time (regeneration from the seed bank) could contribute to recolonization (Husband & Barrett 1996). However, no studies have so far described the relative contribution of dispersal in space and time in plant populations. Through sampling the seed-bank and above-ground cohort in natural populations of *A. thaliana* over several years, it was possible to measure the level of migration within (dispersal in time) and between (immigration) populations. Evidence of immigration of seeds and/or pollen from other populations was observed in 49 out of 222 study cohorts, yielding an average migration rate of 1.8% per generation. Dispersal through seeds was considerably higher than pollen dispersal, with an average seed to pollen ratio being 7.06 across 10 populations. The estimated migration rate is considerably higher than what we may expected from the high F_{ST} values found across populations. The inconsistency between high population differentiation and high migration rate could be due to large effect of random genetic drift in purging rare migrants. However, one may expect a high migration rate for a weedy species that inhabits disturbed areas with a large anthropogenic impact. Moreover, some closely situated populations (< 1 km) were highly differentiated, suggesting the possible role of other factors such as long distance seed dispersal due to anthropogenic activities. Long distance dispersal has also been reported in other studies on *A. thaliana* that found common

multilocus genotypes were shared between populations (Bomblies *et al.* 2010; Lewandowska-Sabat *et al.* 2010).

Additionally dispersal in time was observed in one third of populations (10 out of 29) in which 29 % of seeds on average descended from two or three years before present. The average generation time for these populations exhibiting dispersal in time was 1.5 years. This is lower than the estimates based on historical effective population size (average 4 years). The discrepancy between two estimates is probably due to the fact that historical N_e reflects allelic variation over a long period relative to estimates based on short-term temporal sampling. In populations where no plants in the above ground were observed during field work in a given year, recolonization happened the subsequent year, likely due to regeneration from seed bank. This indicates a significant contribution of seed band to population dynamic in Norwegian population of *A. thaliana*. In many cases a high fluctuation in genetic diversity between years observed in genetically diverse populations is mostly attributed to the variation in regeneration of distinct multilocus genotypes, MLGs, from the seed bank. The average between-year population differentiation was low (F_{ST} = 0.095). This was lower than that recently reported for *A. thaliana* surveyed over four years in southern Europe (F_{ST} = 0.16, Gomaa *et al.* 2011). In some populations the two most frequent MLGs were differentiated at only one SNP site, indicating a mutation as the source of variation. In addition, signature of historical recombination events was observed through the presence of all four possible allele combinations at two-locus haplotype in several populations (sensu Stumpf & McVean 2003). The results indicate that the current pattern of genetic variation in natural populations of *A. thaliana* in Norway is shaped by historical events such as mutation, colonization and recombination. Despite of frequent migrations events through seed and pollen dispersal in the natural populations of *A. thaliana,* seed bank play a substantial role in overall population dynamic.

Patterns of genetic diversity and structure of A. lyrata in contrasting regions (Paper IV)

Patterns of genetic diversity and differentiation in natural populations of *A. lyrata* were compared between three regions in northern Europe. The level of genetic differentiation among Icelandic populations (F_{ST} = 0.1; mean geographical distance 93 km, range 8.6-182 km) was smaller than observed for Swedish (F_{ST} = 0.19; mean geographical distance 40 km,

range 2-85 km) and Norwegian (F_{ST} = 0.30: mean geographical distance 165 km, range 2-385 km) populations. Additionally genetic differentiation among populations distributed over similar area in Icelandic was still considerably lower compared to Swedish and Norwegian populations. Genetic diversity in Icelandic populations (H_E = 0.35) was similar to that observed in Sweden (H_E = 0.33), and both were substantially higher than what found in Norwegian populations (H_E = 0.25). The discrepancy in the level of genetic diversity between regions is probably due to a high allelic richness in the Icelandic and Swedish populations compared with Norwegian ones. A significant relationship between genetic and geographical distance was observed in Icelandic populations (r = 55, P = 001) indicating a pattern of isolation by distance (IBD) and IBD was also evident in Norway and Sweden. However, the slope of the regression line (b) was steeper in Norwegian (b = 0.44) and Icelandic (b = 0.45) populations compared to Swedish (b = 0.15) populations. The observed pattern of IBD in Icelandic populations of *A. lyrata* is inconsistent to what Schierup *et al*. (2008) found when examining the self-incompatibility gene, *S*-locus. The observed IBD pattern at neutral markers is as expected because it has been shown that gene flow by both seed and pollen dispersal is restricted in *A. lyrata* (Schierup *et al.* 2006). IBD in natural populations of *A. lyrata* has also been documented in other studies, at both a local (Clauss & Mitchell-Olds 2006; Gaudeul *et al.* 2007) and continental scale (Muller *et al.* 2008; Ansell *et al.* 2010; Lloyd *et al.* 2011).

Interestingly, there was no significant differences in historical migration rate, M ($M = m/u$, where m and u are immigration and mutation rate per generation respectively) between regions. However, historical effective size measured based on theta (θ) was significantly larger in Icelandic than Swedish and Norwegian populations. The discrepancy between similar levels of genetic diversity, but considerably different historical sizes is probably due to higher private allelic richness found in Icelandic compared with Swedish populations. Icelandic populations, with low levels of population differentiation, exhibit larger effective population sizes compared to Scandinavian populations. It is therefore likely that the low level of population structure (F_{ST}) in Icelandic populations can be explained by a high historical effective population size, rather than high levels of gene flow.

Conclusions and further remarks

The results of this study show that both *A. thaliana* and *A. lyrata* maintain seed banks, preserve genetic variation and increase the effective population size in their distribution range in Norway. However, the investment in the seed bank is considerably higher in *A. thaliana* than in *A. Lyrata*, and is consistent with other studies showing high seed bank density in annuals relative to perennials. Rapid germination of *A. lyrata* seeds probably leads to low seed bank densities, while the large seed size limits the dispersal ability.

In *A. thaliana*, the results indicate that populations experience a relatively high degree of immigration from other populations (dispersal in space), a pattern which is expected from a weedy species inhabiting disturbed habitats impacted by human activities. Moreover, one third of the populations exhibit dispersal in time. Further studies should be aimed at understanding the molecular mechanisms of this. This is the first study that attempts to estimate real-time migration rate and dispersal in time in plant populations. More studies are therefore needed to test whether the observed pattern is valid for other plants, and to develop better models to understand the process.

Comparing patterns of genetic diversity and structure in *A. lyrata* populations from different regions revealed extremely low population differentiation among Icelandic populations compared to in Scandinavia. This pattern is more likely due to large effective population size rather than immigration *per se*, and this suggests that comparing patterns of genetic structure between habitats could be a powerful approach to understand the evolutionary mechanisms behind the current distribution of plant species.

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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*

1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors

1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis

1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems

2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar

2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania

2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease

2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in *Arabidopsis thaliana*

2011	Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds