

Bibliography on *Silene* species – related to pollination biology

The list contains about 300 entries (March 2004). However, it is certainly not complete and focusses mainly on pollination biology.

TW = key words given by Taina Witt

- Aeschimann, D. (1984). "Etude biosystématique du *Silene vulgaris* s.l. (Caryophyllaceae) dans le domaine alpin. Morphologie de la graine." *Candollea* 39: 135-149.
TW; *Silene*; Caryophyllaceae; morphology; seed; testa; systematics; taxonomy; alpine; demography
- Akeroyd, J. R. (1988). "Taxonomic notes on *Silene* L." *Botanical Journal of the Linnean Society* 97: 338-342.
TW; *Silene*; Caryophyllaceae; taxonomy; systematics
- Akhter, S. and J. Antonovics (1999). "Use of internal transcribed spacer primers and fungicide treatments to study the anther-smut disease, *Microbotryum violaceum* (= *Ustilago violacea*), of white campion *Silene alba* (= *Silene latifolia*)." *International Journal of Plant Sciences* 160(6): 1171-1176.
TW; ITS; *Ustilago*; demography; infection; resistance; patterns; genetics; *Silene*; Caryophyllaceae; Ustilaginales; Mycophyta
We report the construction and use of polymerase chain reaction (PCR) primers for detection of *Microbotryum violaceum* in *Silene alba*. Such primers show that the pathogen is present in the aboveground bud meristems, flower pedicels, and flower-stem internodes but not in the flowering-stem leaves and roots of flowering plants. Use of primers also showed that the pathogen was absent from plants that had been inoculated with the fungus but remained healthy. The fungicides Folicur and Bayleton cured plants of the disease, and the absence of the fungus from such cured plants; was confirmed using the PCR primers.
- Alatalo, J. M. (1997). "Gender lability in trioecious *Silene acaulis* (Caryophyllaceae)." *Nordic Journal of Botany* 17: 181-183.
TW; Caryophyllaceae; *Silene*; trioecy; sex; reproduction; breeding system
- Alatalo, J. M. and U. Molau (1995). "Effect of altitude on the sex ratio in populations of *Silene acaulis* (Caryophyllaceae)." *Nordic Journal of Botany* 15(3): 251-256.
TW; sex ratio; Caryophyllaceae; ecology; *Silene*; reproduction; sex
- Alatalo, J. M. and U. Molau (2001). "Pollen viability and limitation of seed production in a population of the circumpolar cushion plant, *Silene acaulis* (Caryophyllaceae)." *Nordic Journal of Botany* 21(4): 365-372.
TW; reproduction; pollination; Caryophyllaceae; *Silene*; sex; dioecy
Pollen viability among genders and limitation of female seed production in a natural trioecious population of the circumpolar cushion plant *Silene acaulis* was examined. Pollen viability was estimated by an in vitro pollen germination experiment. Both male and hermaphrodite flowers displayed large variation in pollen viability (0-53% in hermaphrodite and 0-54% in male flowers). There was a significant difference between genders in pollen viability: male plants had on average higher pollen viability than hermaphrodite plants. Resource and pollen limitation of seed production was studied by an experiment consisting of three treatments; (I) hand-pollination and removal of all other flowers on the cushion, (II) hand-pollination without removal of other flowers, and (III) open pollination without removal of flowers. Hand-pollination increased seed production, whereas removal of flowers had no effect on seed production. Abortion of pollinated ovules during seed development and seed mass did not differ among treatments. To control for effect of fruit number on seed production, data from naturally pollinated individuals was used. There was a positive correlation between both total number of seeds and fruit number, mean seed number per fruit and fruit number, respectively. These results indicate that seed production of *S. acaulis* is mainly limited by pollen availability whereas resource competition between fruits is not important as a limiting factor. The possible role of male quality differences between genders and pollen limitation of seed production for maintenance of trioecious reproductive systems is discussed.
- Alatalo, J. M. and O. Totland (1997). "Response to simulated climatic change in an alpine and subarctic pollen-risk strategist, *Silene acaulis*." *Global Change Biology* 3(Supp. 1): 74-79.

TW; climate; ITEX; subarctic; alpine; flowering phenology; Caryophyllaceae; temperature; *Silene*; reproduction; seed set; ecology; alpine; arctic; global change;

The aim of this study was to test if early no overing species respond with increased seed production to climate warming as is predicted for late-flowering seed-risk strategists. Experimental climate warming of about 3 degrees C was applied to two populations of the cushion-forming plant *Silene acaulis* (L.) Jacq. The experiment was run at one subarctic site and one alpine site for 2 years and 1 year, respectively, using open-top chambers (OTC). The 2-year temperature enhancement at the subarctic site had a marked effect on the flowering phenology. Cushions inside the OTC started flowering substantially earlier than control cushions. Both the male and female phases developed faster in the OTCs, and maturation of capsules occurred earlier. The cushions also responded positively in reproductive terms and produced more mature seeds and had a higher seed/ovule ratio. After 1 year temperature enhancement at the alpine site there was a weak trend for earlier flowering, but there was no significant difference in seed production or seed/ovule ratio.

Altizer, S. M., P. H. Thrall, et al. (1998). "Vector behavior and the transmission of anther-smut infection in *Silene alba*." *American Midland Naturalist* 139(1): 147-163.

TW; population; disease spread; dispersal; patterns; host pathogen interaction; models; *Silene*; Caryophyllaceae; Ustilaginales; pollination; parasitism

Anther-smut disease caused by *Ustilago violacea* is transmitted by insects that visit diseased flowers and then deposit spores on healthy *Silene alba* plants. The transmission rate of this disease therefore depends on spore deposition by the vector species and preferences for infected vs. Healthy hosts. We observed natural populations of *S. alba* to document the most abundant insect visitors, which include syrphid flies, andrenid bees, bumblebees and a variety of nocturnal moths. Using bumblebees and moths in flower preference studies, we showed that bumblebees preferentially visited healthy flowers, but the strength of this preference declined if the bees had prior exposure to diseased flowers. Nocturnal moths showed less discrimination with respect to disease status when plants were arranged in a field population of *S. alba*, and preferentially visited plants with more flowers. A laboratory analysis of spore deposition by bumblebees showed that whereas most spores were deposited on the first several flowers visited, flowers beyond the 15th visit may still receive enough spores to produce a new infection. Spore deposition was also influenced by changes in vector behavior associated with spacing in artificial arrays of *S. alba* plants. Models were fitted to deposition data to compare estimates for spore dispersal rates and the initial number of spores acquired by vectors. This study demonstrated several ways that vector behavior can influence rates of disease spread in natural populations. Preferences for healthy vs. Infected hosts can cause disease dispersal to vary from that expected by randomly foraging insect vectors. Changes in visitation behavior associated with host density can affect the magnitude and distance of spore deposition in host populations.

Andersson, S., L. A. Nilsson, et al. (2002). "Floral scents in butterfly-pollinated plants: possible convergence in chemical composition." *Botanical Journal of the Linnean Society* 140(2): 129-153.

TW; scent; flower; Lepidoptera; psychophily; pollinator attraction; pollinator behavior; GC MS; linalool; benzenoids; Caryophyllaceae; *Dianthus*; *Agrostemma*; *Silene*; Asteraceae; Dipsacaceae; Gentianaceae; Lamiaceae; Loganiaceae; Orchidaceae; Polemoniaceae; Primulaceae; Rubiaceae; Thymelaeaceae; Valerianaceae; Verbenaceae; adaptation

The study explores whether or not there are convergent patterns in floral scent composition among plant species that completely or partially rely on butterflies for pollination. Floral scent compounds were analysed from 22 flowering butterfly-pollinated plant species, representing 13 families which originate mainly from temperate North Europe but also from tropical and temperate America. Scents were collected using the dynamic headspace adsorption method and identified with coupled gas chromatography and mass spectrometry (GC-MS). In total, 217 floral scent compounds were identified, with the number per species ranging from 8 to 65. The major emerging pattern is the occurrence of certain compounds emitted exclusively by the flowers of many of the investigated species in major amounts - the benzenoids phenylacetaldehyde and 2-phenylethanol, the monoterpenes linalool and linalool oxide (furanoid) I and II and the irregular terpene oxoisophorone. It is likely that these compounds serve as a signal to attract pollinating butterflies, and may have evolved in conjunction with the sensory capabilities of butterflies as a specific group of pollinators. While there is convergence in terms of the compounds sharing this function there has been a geographical divergence in terms of their relative abundance. The predominance (in terms of both numbers and relative amount) of benzenoids in many of the scent blends of the European temperate species and of linalool and its derivatives in those of the American species constitute two discernible groups among these plants.

Anonymous "*Silene dioica* (L.) Clairv." 528-529.
TW; *Silene*; ecology; Caryophyllaceae;

Antonovics, J., M. Hood, et al. (2002). "The ecology and genetics of a host shift: *Microbotryum* as a model system." *American Naturalist* 160: S40-S53.

parasitism; Ustilaginales; *Silene*; disease spread; coevolution; resistance; infection; pathogen; evolution; Caryophyllaceae

The need to prevent and cure emerging diseases often precludes their continuing study in situ. We present studies on the process of disease emergence by host shifts using the model system of anther-smut disease (*Microbotryum violaceum*) on the plant genus *Silene* (Caryophyllaceae). This system has little direct social impact, and it is readily amenable to experimental manipulation. Our microevolutionary studies have focused on the host shift of *Microbotryum* from *Silene alba* (= *latifolia*; white campion) onto *Silene vulgaris* (bladder campion) in a population in Virginia. Karyotypic variation shows that the host shift is recent and originates from the disease on sympatric *S. alba*. Analysis of the spatial pattern of disease shows that the host shift has been contingent on the co-occurrence of the two species at a local scale. Cross- inoculation studies show that families of the new host differ greatly in their susceptibility to the pathogen, indicating the potential for rapid evolution of resistance. Disease expression on the new host is frequently abnormal, suggesting that the pathogen is imperfectly adapted to its new host. In experimental populations, disease transmission within populations of the old host is greater than within populations of the new host. However, there is also a high transmission rate of the disease from the new host back to the old host, suggesting a feedback effect that increases disease prevalence in the community as a whole. Continuing studies of these populations are designed to determine whether this new host- pathogen system is likely to be self-sustaining and to quantify evolutionary changes in both the host and the pathogen.

Antonovics, J., M. E. Hood, et al. (2003). "Herbarium studies on the distribution of anther-smut fungus (*Microbotryum violaceum*) and *Silene* species (Caryophyllaceae) in the eastern United States." *American Journal of Botany* 90(10): 1522-1531.

Caryophyllaceae; pathogen; invasion; Ustilaginales; distribution; *Silene*; North America; herbaria; methods

We used herbarium specimens of *Silene virginica*, *S. caroliniana*, *S. rotundifolia*, and *S. latifolia* to survey the incidence of anther-smut disease (caused by *Microbotryum violaceum* sensu lato) in the eastern USA. We found no evidence of a collector bias against diseased specimens. Diseased specimens were frequently found in collections of *S. virginica* and *S. caroliniana*, but not in those of *S. rotundifolia* or *S. latifolia*. Disease incidence in *S. virginica* and *S. caroliniana* increased significantly over the past century and was higher in marginal populations. The absence of disease in specimens of *S. rotundifolia* is consistent with field observations. but its presence in natural populations of *S. latifolia* (especially in Virginia) suggests that the disease is recently introduced. Changes in the host distributions were also evident. The relative abundance of *S. caroliniana* declined over time (especially further north), while the relative abundance of *S. virginica* increased. *Silene latifolia* was absent or rare south of Pennsylvania before ca. 1920. indicating that *S. latifolia* and its anther smut are likely to be recent introductions in Virginia. Methods are also presented that quantify the completeness of coverage provided by herbarium specimens.

Aspi, J., A. Jakalaniemi, et al. (2003). "Multilevel phenotypic selection on morphological characters in a metapopulation of *Silene tatarica*." *Evolution* 57(3): 509-517.

selection; herbivory; pollination; gradient; *Silene*; Caryophyllaceae; morphology; evolution; ecology; habitat

This study partitions selection in a natural metapopulation of a riparian plant species, *Silene tatarica*, into individual- and patch-level components by using contextual analysis, in which a patch refers to a spatially distinct stand of individual plants. We estimated selection gradients for two morphological characters (plant height and number of stems), their respective patch means, and plant density with respect to reproductive success in a two-year study. The approach was also extended to partition selection separately within habitats with varying degrees of exposure to river disturbances and herbivory. The selection differentials and gradients for plant height were positive at both individual and patch levels, with selection forces highest in the closed habitat with low exposure to disturbance. This pattern suggests that local groups with taller than average plants are more visible to pollinators than to groups that are shorter than average plants; and, within patches, individuals with short stature are visited less often than taller ones. Selection on the number of stems was in opposition at individual and patch levels. At the individual level the character was selected toward higher values, whereas selection at the patch-level favored smaller mean number of stems. The

strength of the latter component was associated with the intensity of herbivory in different habitats, suggesting that the patch-level selection against a large number of stems might be due to high attractiveness of such patches to the main herbivore, reindeer. Consequently, direction and strength of selection in spatially structured populations may depend significantly on fitness effects arising at the group level.

- Atanassov, I., C. Delichere, et al. (2001). "Analysis and evolution of two functional Y-linked loci in a plant sex chromosome system." *Molecular Biology and Evolution* 18(12): 2162-2168.
White campion (*Silene latifolia*) is one of the few examples of plants with separate sexes and with X and Y Sex chromosomes. The presence or absence of the Y chromosome determines which type of reproductive organs-male or female-will develop. Recently, we characterized the first active gene located on a plant Y chromosome, SIY1, and its X-linked homolog, SIX1. These genes encode WD-repeat proteins likely to be involved in cell proliferation. Here, we report the characterization of a novel Y-linked gene, SIY4, which also has a homolog on the X chromosome, SIX4. Both SIY4 and SIX4 potentially encode fructose-2,6-bisphosphatases. A comparative molecular analysis of the two sex-linked loci (SIY1/SIX1 and SIY4/SIX4) suggests selective constraint on both X- and Y-linked genes and thus that both X- and Y-linked copies are functional. Divergence between SIY4 and SIX4 is much greater than that between the SIY1 and SIX1 genes. These results suggest that, as for human XY-linked genes, the sex-linked plant loci ceased recombining at different times and reveal distinct events in the evolutionary history of the sex chromosomes.
- Audran, J. C. and M. Batcho "Localisation et evolution differentielle du mycelium d'*Ustilago violacea* (Pers.) Rouss. au sein des tissus vegetatifs et reproducteurs de *Silene dioica* (L.) Clairv." 37-50.
TW; *Silene*; Caryophyllaceae; Ustilaginales; parasitism
- Audran, J. C. and M. Batcho (1982). "Comportement d'*Ustilago violacea* (Pers.) Rouss. au sein des tissus végétatifs et reproducteurs du *Silene dioica* (L.) Clairv." *Rev. Cytol. Biol. végét.-Bot.* 5: 59-63.
TW; Ustilaginales; Caryophyllaceae; *Silene*; parasitism
- Audran, J. C., B. Mousset, et al. (1983). "Quatre exemples de castration male chez les Angiospermes." *Ann. Scientifiques de l'Universite de Reims et de l'A.R.E.R.S.* 19: 43-56.
TW; flower; Caryophyllaceae; androecium; *Silene*; breeding system; sex; Fabaceae; morphology
- Baker, A. J. M. and D. H. Dalby (1980). "Morphological variation between some isolated populations of *Silene maritima* within the British Isles with particular reference to inland populations on metalliferous soils." *New Phytologist* 84: 123-138.
TW; morphology; heavy metal; Great Britain; *Silene*; demography; isolation;
- Baker, H. G. (1947). "Infection of species of *Melandrium* by *Ustilago violacea* (Pers.) Fuckel and the transmission of the resultant disease." *Annals of Botany* XI: 333-348.
Mycophyta; *Silene*; Caryophyllaceae; Ustilaginales; demography; dispersal; TW; parasitism
- Baker, H. G. (1947). "Biological flora of the British Isles, *Melandrium* (Roehling em.) Fris." *Journal of Ecology* 35: 271-292.
TW; Flora; *Silene*; Caryophyllaceae; pollination; ecology
- Baker, H. G. (1948). "Stages in invasion and replacement demonstrated by species of *Melandrium*." *Journal of Ecology* 36: 96-119.
TW; *Silene*; Caryophyllaceae; Invasion; demography; Great Britain; Europe; hybrid;
- Baker, H. G. (1948). "The ecotypes of *Melandrium dioicum* (L. emend.) Coss. & Germ." *New Phytologist* 47: 131-145.
TW; *Silene*; Caryophyllaceae; ecology; distribution; hybrid; Europe; demography;
- Baker, H. G. (1961). "The adaptation of flowering plants to nocturnal and crepuscular pollinators." *Quarterly Review of Biology* 36: 64-73.
TW; allogamy; chiropterophily; evolution; Lepidoptera; sphingophily; Sphingidae; Entomophily; behavior; coevolution; pollinator behavior; pollination; ornithophily; *Parkia*; *Ceiba*; tropical; *Silene*; Caryophyllaceae; review; nocturnal
- Baker, H. G. (1966). "The evolution of floral heteromorphism and gynodioecism in *Silene maritima*." *Heredity* 21: 689-692.

TW; gynodioecy; Caryophyllaceae; *Silene*; breeding system; pollination; heteromorphy; evolution; sexual system

Bathori, M., H. Kalasz, et al. (2002). "5-alpha- and 5-beta-2-deoxyintegristerone A, a 5-alpha and 5-beta isomer pair of ecdysteroids isolated from the *Silene* genus." *Biomedical Chromatography* 16(6): 373-378.

TW; Caryophyllaceae; *Silene*; steroid hormones; compounds; leaf
5-Alpha-2-deoxyintegristerone A and 5-beta-2-deoxyintegristerone A were isolated from the aerial parts of *Silene italica* ssp. *nemoralis* (Waldst. and Kit.) Nyman using a specific combination of absorption column chromatography, preparative thin-layer chromatography and preparative HPLC. Both normal-phase and reversed-phase modes of HPLC were employed for isolation. Structural elucidation of 5-alpha-2-deoxyintegristerone A was completed by X-ray diffraction. Both 5-alpha-2-deoxyintegristerone A and 5-beta-2-deoxyintegristerone A were firstly isolated from this plant. We propose that 5-alpha-2-deoxyintegristerone A is not an artifact but an integral part of the ecdysteroid spectrum of *Silene italica* ssp. *nemoralis* (Waldst. and Kit.) Nyman. Copyright (C) 2002 John Wiley Sons, Ltd.

Becherer, A. (1963). "Über *Silene insubrica* Gaudin." *Verhandlungen der Schweizerischen Naturforschenden Gesellschaft* 142: 105.

TW; *Silene*; Caryophyllaceae;

Berge, G., I. Nordal, et al. (1998). "The effect of breeding systems and pollination vectors on the genetic variation of small plant populations within an agricultural landscape." *Oikos* 81(1): 17-29.

TW; demography; Caryophyllaceae; breeding system; genetics; population; pollination; Poaceae; gene flow; Brassicaceae; isozymes; pollinator behavior; anemogamy; entomophily; xenogamy; autogamy; autogamy; xenogamy

Within an agricultural landscape (approximately 8 km²) the genetic structures of the herbs *Festuca ovina*, *Lychnis viscaria* and *Arabis thaliana* were examined using isoenzymes. The species have different breeding systems and pollination vectors, and occur in small populations in remnant patches of semi-natural habitats throughout the landscape. There was no or only a weak correlation between population size and genetic diversity. The wind-pollinated, outcrossing species *F. ovina* had the highest levels of genetic variation, intermediate levels were found in the largely xenogamy and insect pollinated *L. viscaria*, while lowest levels of variation were found in the inbreeding *A. thaliana*. Relative to their breeding systems and the small geographical scale of the study all species exhibited remarkably high levels of total genetic variation. In the outbreeding species most of the genetic variation was found within populations (*F. ovina*: FST = 0.059 and *L. viscaria*: FST = 0.092). No geographic pattern was found between populations in the outbreeding species, indicating high levels of gene flow. The cereal fields separating the populations may function as conduits rather than barriers to pollen dispersed by wind, and pollinating insects (bumblebees and butterflies) may have no problems moving between patches at this scale, thus alleviating the danger of genetic erosion associated with small population size. In contrast, the fields appear to be efficient barriers to gene flow by seed dispersal. In the inbreeding *Arabis thaliana* a geographic pattern was evident. Most of the variation in this species was found between populations (FST = 0.722) indicating low levels of gene flow; single populations exhibited large variation in the number of genotypes present (1 to 15).

Biere, A. (1991). "Parental effects in *Lychnis flos-cuculi*. I. Seed size, germination and seedling performance in a controlled environment." *Journal of Evolutionary Biology* 3: 447-465.

TW; Caryophyllaceae; seed; germination; reproduction; paternity analysis; size; seedling; fitness

Biere, A. and J. Antonovics (1996). "Sex-specific costs of resistance to the fungal pathogen *Ustilago violacea* (*Microbotryum violaceum*) in *Silene alba*." *Evolution* 50: 1098-1110.

TW; sex; costs; Mycophyta; Ustilaginales; *Silene*; Caryophyllaceae; parasitism

Biere, A., R. Cappers, et al. (1989). "Quantitative and qualitative aspects of fecundity in *Lychnis flos-cuculi*." *Acta Botanica Neerlandica* 38: 203-218.

TW; fruit set; reproduction; seed set; flowering phenology; Caryophyllaceae; success; pollination

Biere, A., J. A. Elzinga, et al. (2002). "A plant pathogen reduces the enemy-free space of an insect herbivore on a shared host plant." *Proceedings of the Royal Society of London Series B-Biological Sciences* 269(1506): 2197-2204.

interaction; pathogen; Ustilaginales; *Silene*; Caryophyllaceae;

An important mechanism in stabilizing tightly linked host- parasitoid and prey-predator interactions is the presence of refuges that protect organisms from their natural enemies. However, the presence and quality of refuges can be strongly affected by the environment. We show that infection of the host plant *Silene latifolia* by its specialist fungal plant pathogen *Microbotryum violaceum* dramatically alters the enemy-free space of a herbivore, the specialist noctuid seed predator *Hadena bicruris*, on their shared host plant. The pathogen arrests the development of seed capsules that serve as refuges for the herbivore's offspring against the specialist parasitoid *Microplitis tristis*, a major source of mortality of *H. bicruris* in the field. Pathogen infection resulted both in lower host-plant food quality, causing reduced adult emergence, and in twofold higher rates of parasitism of the herbivore. We interpret the strong oviposition preference of *H. bicruris* for uninfected plants in the field as an adaptive response, positioning offspring on refuge-rich, high-quality hosts. To our knowledge, this is the first demonstration that plant- inhabiting micro-organisms can affect higher trophic interactions through alteration of host refuge quality. We speculate that such interference can potentially destabilize tightly linked multitrophic interactions.

- Biere, A. and S. J. Honders (1996). "Impact of flowering phenology of *Silene alba* and *S. dioica* on susceptibility to fungal infection and seed predation." *Oikos* 77: 467-480.
 TW; phenology; flowering phenology; *Silene*; Caryophyllaceae; predation; Noctuidae; reproduction; seed; interaction; coevolution; Mycophyta; Ustilaginales; SB; host pathogen interaction
- Bittrich, V. (1993). Caryophyllaceae. In: K. Kubitzki, J. G. Rohwer and V. Bittrich, The Families and Genera of Vascular Plants. Berlin, Heidelberg, New York, Springer. Vol. II, Flowering Plants: 206-236.
 TW; Caryophyllaceae; *Silene*; systematics; taxonomy; pollination; morphology; anatomy; phenology; key
- Blake, E. A., P. R. Wallis, et al. (1976). "The Red German Catchfly on the Western Ochil Hills." *Forth Naturalist and Historian* 1: 117-121.
 TW; Caryophyllaceae; pollination; Europe; Great Britain; *Lychnis*
- Bland, K. P. (1994). "*Silene acaulis* (L.) Jacq. (Caryophyllaceae), the larval foodplant of *Delia piliventris* (Pok.) (Diptera Anthomyiidae)." *Br. J. Ent. Nat. Hist.* 7: 77-79.
 TW; *Silene*; interaction; herbivory; predation; Caryophyllaceae; Diptera; parasitism
- Bocquet, G. (1968). "Cléistogamie et évolution chez les *Silene* L. sect. *Physolychnis* (Benth.) Bocquet (Caryophyllaceae)." *Candollea* 23: 67-80.
 TW; phenology; cleistogamy; autogamy; *Silene*; Caryophyllaceae; breeding system; evolution; systematics; taxonomy;
- Bopp, S. (1999). "Peculiarities of the inner calyx surface of caryophylloideae with special regard to sexual dimorphism in two dioecious species." *Plant Biology* 1(2): 207-213.
 TW; Caryophyllaceae; *Silene*; morphology; dimorphism; flower; electronmicroscopy; REM; Trichome; calyx; dioecy; compounds; predation; seed predation; host pathogen interaction; Lepidoptera; oviposition; evolution; reproduction; Noctuidae; *Hadena*
 The structure of the inner calyx surface of several *Silene* and one *Saponaria* species with different sex expression have been investigated by scanning electron microscopy. Some of the hermaphroditic and gynodioecious species show peculiarities in the basal parts of their calyces, such as cylindrical trichomes in *S. nutans*. Capitate trichomes occur exclusively on the inner calyx surface of the two dioecious species *S. dioica* and *S. latifolia* ssp. *alba*. In both species the density of these trichomes is significantly higher in female than in male individuals. The hypothesis is proposed that these trichomes play a role in flower discrimination of specialized pollinators and seed predators.
- Bopp, S., T. Witt, et al. (1999). Phänologische Untersuchungen an *Silene latifolia* ssp. *alba* und *Silene dioica* (Caryophyllaceae). 14. Symposium Biodiversität & Evolutionsbiologie, Jena.
 TW; Caryophyllaceae; *Silene*; phenology
- Bouquet-Bonnet, S., M. Rochd, et al. (2002). "Total assignment of H-1 and C-13 NMR spectra of three triterpene saponins from roots of *Silene vulgaris* (Moench) Garcke." *Magnetic Resonance in Chemistry* 40(9): 618-621.
Silene; compounds; Caryophyllaceae; root
 The assignments of H-1 and C-13 NMR spectra for three new triterpene saponins from *Silene vulgaris* (gypsogenin 3-O- glucuronide, quillaic acid 3-O-glucuronide, and gypsogenin 3-O-

glycoside) are reported. In addition to ID NMR methods, 2D NMR techniques (COSY, HSQC, HMBC, and HSQC-TOCSY) were used for the assignments. Copyright (C) 2002 John Wiley Sons, Ltd.

- Brantjes, N. B. M. (1973). Sphingophilous flowers, function of their scent.
TW; Sphingidae; Lepidoptera; pollinator behavior; Caryophyllaceae; *Silene*; scent; sphingophily;
- Brantjes, N. B. M. (1976). "Riddles around the pollination of *Melandrium album* (Mill.) Garcke (Caryophyllaceae) during the oviposition by *Hadena bicruris* Hufn. (Noctuidae). II." Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C 79: 13.
TW; *Silene*; sphingophily; pollination; Caryophyllaceae; Noctuidae; floral traits; scent; pollinator behavior; predation; coevolution; interaction; oviposition; parasitism
- Brantjes, N. B. M. (1976). "Senses involved in the visiting of flowers by *Cucullia umbratica* (Noctuidae, Lepidoptera)." Ent. exp. & appl. 20: 1.
TW; senses; pollination; olfactory; pollinator behavior; predation; Noctuidae; Lepidoptera; *Silene*; Caryophyllaceae; Europe
- Brantjes, N. B. M. (1976). "Prevention of superparasitism of *Melandrium* flowers (Caryophyllaceae) by *Hadena* (Lepidoptera)." Oecologia 24: 1.
TW; *Silene*; Caryophyllaceae; Noctuidae; interaction; herbivory; Lepidoptera; pollination; Europe; parasitism
- Brantjes, N. B. M. (1976). "Riddles around the pollination of *Melandrium album* (Mill.) Garcke (Caryophyllaceae) during the oviposition by *Hadena bicruris* Hufn. (Noctuidae). I." Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C 79: 1-12.
TW; *Silene*; sphingophily; pollination; Caryophyllaceae; Noctuidae; floral traits; scent; pollinator behavior; predation; coevolution; interaction; oviposition; parasitism
Larvae of *H. bicruris* are seed-predators on *M. album*. The adults use the flowers to feed on nectar and to oviposit. Both activities are described in detail. For oviposition which takes place exclusively into pistillate flowers, an extendible ovipositor is inserted into the flowertube. The egg is mostly attached to the ovary. Scent provokes the moth to perform a characteristic seeking-flight. Apart from the visual means the moths are able to locate flowers by smell alone. The moth is first attracted and then decides by the smell whether or not to land. Tests show the number of landings on objects is proportional to scent intensity. Extracts of staminate and pistillate flowers receive the same number of visits and apparently have an equal odor intensity. Neither calyx, stigma, ovary or the amount of nectar in the flowers are significant for distinguishing between pistillate and staminate flowers by the ovipositing moth, but petals, the ligula as well as the lobe, are important. Selection of the oviposition site may be determined by smell alone. There is a quantitative relation between the number of petals and the probability to receive eggs. The feeding and the oviposition behavior are interrelated and appear as 1 complex behavior. The oviposition act is always preceded by drinking from the flower, which becomes pollinated in the process. When the drinking is prevented by satiation of the moth, selectivity with regard to oviposition site is lost. The perception of flower type takes place in the time interval between the finding of a flower and the insertion of the proboscis. Associations, formed during drinking, influence the selection of oviposition site. The innate preference to oviposit into *M. album* flowers is stronger than known associations with other flower species. Nectar consumption is necessary for a steady egg production; a moth consumes about 23 μ l each night. To obtain this quantity, approximately 100 flowers have to be visited. A moth pair will pollinate up to a maximum of 500 pistillate flowers, during their life time. The progeny of 1 moth pair can destroy more than 500 seed capsules; *H. bicruris* is not a symbiont but a real predator of *M. album*.
- Brantjes, N. B. M. (1976). "Riddles around the pollination of *Melandrium album* (Caryophyllaceae) during the oviposition by *Hadena bicruris* (Noctuidae, Lepidoptera) Part 2." Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C 79(2): 127-141.
TW; Caryophyllaceae; *Silene*; *Hadena*; oviposition; parasitism; pollination; interaction; predation; pollinator behavior
Both oviposition and visits to flowers by *H. bicruris* can be compared with those of other Lepidoptera, but 1 aspect remains unique for *H. bicruris*. For all other Lepidoptera both activities are separated, but for *H. bicruris* and presumably also for its near relatives, both activities are connected in one complex behavior pattern. This fixed combination has very important consequences for the moth. Pollination results in food for the young being available at the right time. This offers an important survival value for the species. The only known analogy in the Lepidoptera is the relation of

Yucca moth with Yucca flowers. This relationship is a form of real symbiosis, with benefit both for moth and for plant. To *H. bicruris* the relationship is always profitable. Adults feed from the flowers and the larvae eat the seeds. The relationship, therefore, is a form of predation by the moth. It differs significantly from the balanced relationship of the Yucca moth with Yucca flowers. *M. album* survives because each plant lives for several years and because there are often some capsules overlooked by the caterpillars. Other moth species also provide pollination.

Brantjes, N. B. M. (1978). "Sensory responses to flowers in night-flying moths." Linnean Society Symposium Series 6: 13-19.

TW; pollination; senses; interaction; Lepidoptera; predation; oviposition; *Silene*; wind tunnel; Noctuidae; sphingophily; scent; nocturnal; olfactory

Brantjes, N. B. M. and J. A. A. M. Leemans (1976). "*Silene otites* (Caryophyllaceae) pollinated by nocturnal Lepidoptera and Mosquitoes." Acta Botanica Neerlandica 25: 281-295.

TW; Europe; Netherlands; pollination; Diptera; Lepidoptera; sphingophily; Caryophyllaceae; *Silene*; Noctuidae; nocturnal;

S. otites in the dunes in The Netherlands (coastal plants), with wind pollination in addition to insect pollination were studied. Morphological evidence, such as stickyness of pollen, together with field observations on the wind dispersal of pollen and experiments with bagged flowers, prove the absence of wind pollination. Insect visitors belonged mainly to the Lepidoptera (Microlepidoptera, Geometridae and Noctuidae) and to the Diptera (Culicidae). Observations of dusting with pollen and of flower visiting behavior indicate insect pollination. This was proved by experimental confinement of insects with bagged flowers. Neuroptera are visitors but are not pollinators. The pollination of flowers by mosquitoes is new for Europe.

Brockmann, I. and G. Boquet (1978). "Ökologische Einflüsse auf die Geschlechterverteilung bei *Silene vulgaris* (Moench) Garcke (Caryophyllaceae)." Berichte der Deutschen Botanischen Gesellschaft 91: 217-230.

TW; EM; sex; gynodioecy; Caryophyllaceae; *Silene*; sexual system; ecology; statistics;

Brown, E. and S. Kephart (1999). "Variability in pollen load: Implications for reproduction and seedling vigor in a rare plant, *Silene douglasii* var. *oraria*." International Journal of Plant Sciences 160(6): 1145-1152.

TW; pollen limitation; pollen loads; pollination; fitness; pollen; endemism; *Silene*; reproduction; habitat; fragmentation; Caryophyllaceae; North America; USA; breeding system; autogamy; autogamy

Habitat fragmentation can markedly influence the levels of pollen deposition and seed production in natural populations, and rare plants may be especially susceptible to any associated reductions in pollen quantity and quality. In order to ascertain the potential for pollen limitation of maternal fitness in a rare plant, *Silene douglasii* var. *oraria*, which is endemic to western coastal prairies, we counted ovules and measured conspecific and heterospecific pollen deposition on stigmas collected from open-pollinated plants. We further investigated the effect of increasing pollen intensity on fruit production, seed number and weight, as well as several measures of progeny vigor. Three levels of outcross pollen were added to plant stigmas for comparison with autogamous and open pollination in the largest naturally occurring population. Both seed and fruit production were significantly greater ($P < 0.05$) for supplemented versus nonsupplemented stigmas, but flowers receiving different levels of pollen addition were statistically indistinguishable. Seed germination and seedling survival were also lowest for the offspring of nonsupplemented flowers; however, in natural populations, opportunities for pollen competition are very limited since open-pollinated flowers averaged fewer viable pollen grains than ovules. Seed production was equivalent for open- and autogamously pollinated flowers in 1996, indicating that natural pollen transfer may have involved mostly self pollen. Overall, the low reproductive success of var. *oraria* likely reflects both low pollen quantity and quality. Multiyear empirical studies of pollen intensity in field populations are needed so that we can better understand the fitness consequences of pollen limitation in rare perennials.

Brown, J. H. and A. Kodric Brown (1979). "Convergence, competition and mimicry in a temperate community of hummingbird pollinated flowers." Ecology 60(5).

pollination; *Silene*; ornithophily; Caryophyllaceae; USA; competition

The pollination ecology of 9 spp. of red, tubular flowers [*Ipomopsis aggregata*, *Penstemon barbatus*, *Castilleja integra*, *C. austromontana*, *Lonicera arizonica*, *Aquilegia friternata*, *Silene laciniata*, *Echinocereus triglochidiatus* and *Lobelia cardinalis*] which bloom together in different combinations in the White Mountains of Arizona, USA was studied. All species were strikingly convergent in floral

color, size and shape. Hummingbirds, the primary pollinators, usually did not visit flower species selectively, and individual birds often simultaneously carried 4 or more species of pollen. Flowers may have competed interspecifically for these shared pollinators, but competition was reduced because character displacement in orientation of anther and stigma resulted in some species using different parts of the bird to transport their pollen. Most flower species secreted nectar at similar rates, particularly when they bloomed together in mixed stands. A population of *L. cardinalis* secreted no nectar; it attracted hummingbirds by mimicking more abundant, nectar-producing species. This temperate flower community, which resembles some associations of convergent Mullerian and Batesian mimics, may have evolved its characteristic convergent structure because the advantages of using similar signals and rewards to share the same hummingbird pollinators outweigh the advantages of diverging to reduce interspecific competition.

- Bucheli, E., B. Gautschi, et al. (2000). "Host-specific differentiation in the anther smut fungus *Microbotryum violaceum* as revealed by microsatellites." *Journal of Evolutionary Biology* 13: 188-198.
TW; Caryophyllaceae; *Silene*; parasitism; interaction; Ustilaginales; pollination; gene flow; demography; isolation; microsatellites
- Bucheli, E., B. Gautschi, et al. (2001). "Differences in population structure of the anther smut fungus *Microbotryum violaceum* on two closely related host species, *Silene latifolia* and *S. dioica*." *Molecular Ecology* 10: 285-294.
TW; *Silene*; parasitism; Ustilaginales; Mycophyta; Caryophyllaceae; demography; breeding system
- Buide, M. L., J. A. Diaz-Peromingo, et al. (2002). "Flowering phenology and female reproductive success in *Silene acutifolia* Link ex Rohrb." *Plant Ecology* 163(1): 93-103.
TW; Caryophyllaceae; flowering phenology; fruit set; selection; seed set; *Silene*
We investigated flowering phenology and female reproductive success in two populations of *Silene acutifolia* in northwest Spain, over one year (population A) or two consecutive years (population B). Flowering phenology was similar in the two populations and two years. However, significant interannual and interindividual variation was detected in flowering start date, flowering finish date, flowering duration, relative flowering intensity, flowering synchrony index, and median flowering date (the date on which half a plant's flowers had opened). The between-year differences may be partly attributable to the fact that the first year was markedly warmer than the second year. The order in which individual plants started flowering was highly consistent between years, which may reflect genetic control and/or microhabitat heterogeneity. Multiple regressions with fruit set or seed set as the response variables indicated that none of the phenology descriptors, or number of flowers, were significant predictors of female reproductive success.
- Buide, M. L. and J. Guitian (2002). "Breeding system in the dichogamous hermaphrodite *Silene acutifolia* (Caryophyllaceae)." *Annals of Botany* 90(6): 691-699.
inbreeding depression; pollen; germination; protandry; self compatibility; *Silene*; Caryophyllaceae; stigma; receptivity; dichogamy; hermaphrodite; breeding system; Iberian Peninsula; protandry
The breeding system of the dichogamous hermaphrodite species *Silene acutifolia*, endemic to north-west Spain and north and central Portugal, is examined. Pollen germinability and style-stigma receptivity were analysed to determine whether protandry is a barrier to self-fertilization. By 48 h after anthesis, pollen germinability had declined to approx. 10 %. The short straight styles are not receptive when flowers first open. They gradually elongate and curve outwards, develop stigma papillae and become receptive. There is no clear separation between stigma and style: the stigma papillae appear in a line along the length of the style. Fruit set is high regardless of pollen source; however, seed set is significantly reduced after both spontaneous and facilitated autogamy. Seed set following spontaneous autogamy was 30 % (86 % in controls) in 1998 and 33 % (87 % in controls) in 1999. Seed set following facilitated autogamy was 62 % (86 % in controls) in 1998 and 67 % (89 % in controls) in 1999. Thus, separation of the male and female phases does not prevent production of seeds by self-pollination, although it does reduce the likelihood of this. Furthermore, results of the present experiments indicate that this species has no self-incompatibility mechanisms (self-compatibility index = 0.98). The selfing rate in the study population was 0.41, which is supported by the lack of self-incompatibility systems and by the incomplete protandry. (C) 2002 Annals of Botany Company.
- Burleigh, J. G. and T. P. Holtsford (2003). "Molecular systematics of the eastern North American *Silene* (Caryophyllaceae): Evidence from nuclear ITS and chloroplast trnL intron sequences." *Rhodora* 105(921): 76-90.

Caryophyllaceae; ITS; evolution; *Silene*; North America; RAPD; molecular systematics; chloroplast; genetics

This study examines the phylogenetic relationships of the nine *Silene* species endemic to eastern North America using nuclear ITS and chloroplast trnL intron sequence data. The ITS region is highly variable among taxa and is more phylogenetically informative than the less variable trnL intron DNA data. The ITS sequences indicate that the eastern North American taxa are not monophyletic, but instead occur in two clades that are nested within a clade including western species. *Silene* section Occidentales is also not monophyletic. The diverse floral morphologies of the eastern North American *Silene* appear to be evolutionarily labile. Neither floral morphology nor pollinator syndromes are conserved within clades. Both ITS and trnL intron data indicate that the hummingbird-pollinated taxa are not monophyletic. There is weak evidence for differences in the nuclear and chloroplast phylogenies that may be a result of reticulate evolution.

Carlsson Graner, U. (1997). "Anther-smut disease in *Silene dioica*. Variation in susceptibility among genotypes and populations, and patterns of disease within populations." *Evolution* 51(5): 1416-1426. TW; EM; genetics; Caryophyllaceae; *Silene*; Ustilaginales; Genotype; host pathogen interaction; Sweden; resistance; infection;

In an archipelago in northern Sweden, populations of the perennial, dioecious, and insect-pollinated herb *Silene dioica* are commonly infected by the sterilising anther-smut fungus *Microbotryum violaceum*. The results from transplantation and inoculation experiments in this study show that variation between populations in the incidence of disease may partly be due to variation in resistance among populations. In the transplantation experiment in which plants were naturally exposed to the fungus, disease levels varied greatly among transplants from three healthy populations when transplanted to three diseased populations in the archipelago. Clear genotypic differences in susceptibility among 25 replicated genotypes of the host plants were found when inoculated manually with two different isolates. Susceptibility varied between 0-90%, but the two isolates used did not differ in inoculation success. The results also suggest a geographical structuring in resistance of the host and virulence of the fungus. First, disease levels among experimental plants from two of the disease-free populations of *S. dioica* (originating from inner and outer archipelago, respectively), were high when transplanted to a diseased population nearby, but low when transplanted far away. Second, regardless of origin, plants from all healthy populations became diseased in the diseased experimental populations located in the middle part of the archipelago. Due to isostatic land upheaval in the studied archipelago, there is a vertical age-axis within islands such that the highest point on an island is the oldest. Since this may affect the demography of the host, disease spread, and the dynamics of disease, spatial patterns in adult and seedling densities, and disease and spore deposition along the age-axis were studied within three diseased populations. A low incidence of disease was found in the young, low and old, high parts of the populations and a high incidence in the vertical, middle parts of the populations. The higher disease incidence in the middle part compared with the lower part of the population may reflect less disturbance and an increased probability of disease with age.

Carlsson Graner, U., T. Elmqvist, et al. (1998). "Floral sex ratios, disease and seed set in dioecious *Silene dioica*." *Journal of Ecology* 86(1): 79-91.

Caryophyllaceae; *Silene*; dioecy; pollination; sex ratio; seed set; parasitism; Ustilaginales

1. In the dioecious, perennial herb *Silene dioica*, the density of pollen donors in a population is determined by overall plant density, the sex ratio and the proportion of plants infected with the anther-smut fungus *Microbotryum violaceum*, which results in permanent sterility of both male and female plants.
2. Pollinators (*Bombus* spp.) were found to prefer male flowers and to avoid diseased flowers. This may result in an overall lower visitation frequency and increased risk for pollen limitation in populations with a low density of males or a high incidence of disease.
3. Compared with open-pollinated flowers, hand pollination resulted in a significant increase in the number of seeds produced per fruit in populations with an experimentally reduced proportion of males (25% and 50% male flowers) but not in a naturally male-dominated population (75% male flowers). Seed production per plant was increased by hand pollination only in the most female-dominated population. Because the floral sex ratio is often male-biased, resources rather than pollen availability are likely to set the upper limit for total seed production per individual in most healthy populations of *S. dioica*.
4. There was a negative relationship between seed set and incidence of disease across 22 populations in both years of a field study. However, there was no consistent difference between the responses of highly diseased populations (incidence 30-56%) and populations with a low disease incidence (incidence 0-8%) to hand pollination.
5. In a greenhouse experiment with cloned hand-pollinated females, the presence of spores on healthy flowers was found to reduce seed set significantly. In highly diseased populations, therefore, the frequent deposition of spores by flower

visitors onto remaining healthy plants may decrease seed production below the potential level determined by resources or pollen availability.

- Carroll, S. B. and L. F. Delph (1996). "The effects of gender and plant architecture on allocation to flowers in dioecious *Silene latifolia* (Caryophyllaceae)." *International Journal of Plant Sciences* 157(4): 493-500.
sex; architecture; resource allocation; dioecy; *Silene*; Caryophyllaceae; sexual system
In dioecious species, reproductive allocation in females and males may differ as a result of the different reproductive functions and needs of the two sexes. In *Silene latifolia* (Caryophyllaceae), males invested a total of 11% more biomass in flowers than females. However, individual female flowers were 2.6 times heavier than individual male flowers (on a dry mass basis), had significantly heavier sepals and pedicels, but not petals, and exceeded male flowers for five linear measures. Individual female flowers also contained 2.7 times more N and 2.9 times more P than individual male flowers. In females, N (on a mg/mg basis) was concentrated in ovules, nectary, petals, and styles and P was concentrated in ovules, nectary, styles, and petals. In males, N and P were concentrated in anthers, antherophor, and petals. Within flowers, the three currencies did not always predict each other, as anthers in males and ovules and styles in females contained higher, while sepals in both sexes contained lower, proportions of both nutrients than of biomass. Flower number was highly influenced by gender, pollination, and architecture. Males produced 2.9 times more flowers than unpollinated females and 14.3 times more flowers than pollinated females. In females, pollination of flowers on one of the two main inflorescence branches significantly reduced the number of flowers produced on that branch, both in comparison to the other inflorescence branch on the same plant and in comparison to the corresponding branch on control plants. Flower number also differed between the two inflorescence branches on control plants, indicating the importance of plant architecture on flower production. It is clear that selection can lead to different reproductive allocation patterns in females and males and that these patterns may vary depending on currency and in response to pollination and architecture in females.
- Carroll, S. B. and D. L. Mulcahy (1991). "The relationship between pollen grain size and progeny gender in dioecious *Silene latifolia* (Caryophyllaceae)." *Sexual Plant Reproduction* 4(3): 203-207.
TW; Caryophyllaceae; *Silene*; dioecy; pollen; pollination; EM; sexual system
Experiments and observations conducted during the past 90 years have provided conflicting evidence concerning the existence of a size difference between pollen grains containing an X chromosome (female-determining) and those containing a Y chromosome (male-determining) in dioecious *Silene latifolia*. Were such a size difference to exist, this might explain, at least in part, the observation that X-bearing pollen tubes reach the ovary more quickly, on average, than Y-bearing pollen tubes. We tested for such a size difference by separating pollen collected from single anthers into three size classes: small, large, and random. Fruit set (number of pollinated flowers that set fruit) and seed set (number of seeds per capsule) did not differ from these three pollination treatments. Progeny sex ratios resulting from these three pollen size classes also did not differ significantly. Thus, pollen grain size is not affected by which of the first direct test of this relationship. Based on our results, size differences should not be invoked to explain competitive differences in male- and female-determining microgametophytes.
- Carroll, S. B. and D. L. Mulcahy (1993). "Progeny sex ratios in dioecious *Silene latifolia* (Caryophyllaceae)." *American Journal of Botany* 80: 551-556.
TW; breeding system; demography; sex; dioecy; *Silene*; Caryophyllaceae; EM;
- Chater, A. O. and S. M. Walters (1964). "Notes on European *Silene*." *Feddes Repertorium* 69: 46-49.
TW; *Silene*; Caryophyllaceae; systematics; taxonomy; Europe
- Chowdhuri, P. K. (1957). "Studies in the genus *Silene*." *Notes of the Royal Botanical Garden Edinburgh* 22: 1-221.
TW; *Silene*; Caryophyllaceae; systematics; taxonomy; evolution; hybrid
- Collin, C. L., P. S. Pennings, et al. (2002). "Natural enemies and sex: how seed predators and pathogens contribute to sex-differential reproductive success in a gynodioecious plant." *Oecologia* 131(1): 94-102.
TW; Caryophyllaceae; *Dianthus*; *Hadena*; *Ustilago*; phenology; pollination; *Silene*; spores; experiment; flowering phenology; oviposition; gynodioecy; seed predation; pathogen; interaction
In insect-pollinated plants flowers must balance the benefits of attracting pollinators with the cost of attracting natural enemies, when these respond to floral traits. This dilemma can have important

evolutionary consequences for mating-system evolution and polymorphisms for floral traits. We investigate the benefits and risks associated with flower size and sex morph variation in *Dianthus sylvestris*, a gynodioecious species with pistillate flowers that are much smaller than perfect flowers. We found that this species is mainly pollinated by nocturnal pollinators, probably moths of the genus *Hadena*, that also oviposit in flowers and whose caterpillars feed on developing fruits and seeds. *Hadena* preferred larger flowers as oviposition sites, and flowers in which *Hadena* had deposited eggs bore more pollen on their stigmas, suggesting that *Hadena* is indeed the principle pollinator, or that pollinators and these seed predators employ the same choice criteria for flowers. Globally, perfect flowers suffered more predation by seed predators than did pistillate flowers, suggesting that seed predators play an important role in reproductive system dynamics in this species. On the other hand, female flowers were more likely to be contaminated with spores of another natural enemy, the pathogenic fungus *Microbotryum violaceum*, that are transmitted by pollinating insects. This complex interplay between two natural enemies, one of which, *Hadena*, is also a pollinator and vector of fungal spores, may contribute to the maintenance of the polymorphic reproductive system of the host plant.

- Colosi, J. C. and P. B. Cavers (1984). "Pollination affects percent biomass allocated to reproduction in *Silene vulgaris* (Bladder Campion)." *American Naturalist* 124: 299-306.
TW; growth; Caryophyllaceae; *Silene*; pollination; biomass
- Comba, L., S. A. Corbet, et al. (1999). "Flowers, nectar and insect visits. Evaluating British plant species for pollinator-friendly gardens." *Annals of Botany* 83(4): 369-383.
TW; pollination; Great Britain; Europe; Botanical Garden; conservation biology; entomophily; melittophily; phalenophily; psychophily; myiophily; Hymenoptera; Apidae; Apis; Bombus; Lepidoptera; Diptera; Syrphidae; nectar; Excretion; Caryophyllaceae; *Saponaria*; *Silene*; Twenty-four plant species native or naturalized in Britain were grown in the Cambridge University Botanic Garden, UK and evaluated as potential resources for nectar-foraging bees, butterflies and hoverflies. In ten plant species a series of measurements were made, at regular intervals from dawn to dusk, of nectar secretion rate and standing crop, and in all species insect visits were monitored throughout daylight hours. The study revealed differences between plant species in the composition of the assemblage of insect visitors, and in the magnitude and temporal distribution of the nectar reward. In some cases we found interesting correlations between temperature and secretion rates or patterns of insect visits. Species that received numerous insect visits in our study are potentially valuable forage plants that might be planted by gardeners to support local pollinator populations. Deep flowers whose nectar is accessible to long-tongued bumblebees (*Bombus hortorum*, *B. pascuorum*) but not to honeybees may provide long-tongued pollinators with a resource refuge relatively free from honeybee competition. Features that make some of those plant species particularly interesting to observe in the garden include robbing by short-tongued bumblebees in *Saponaria*, baseworking by honeybees on closed flowers in *Malva sylvestris*, and apparent displacement of bumblebees by territorial behaviour of the solitary bee *Anthidium manicatum* on species of *Stachys*. (C) 1999 Annals of Botany Company.
- Constantinidis, T., E. P. Barea, et al. (2002). "Karyotaxonomy of Greek serpentine angiosperms." *Botanical Journal of the Linnean Society* 139(1): 109-124.
karyosystematics; distribution; endemism; Greece; karyology; chromosomes; *Silene*; Caryophyllaceae
The chromosome numbers are given for 20 angiosperm taxa, most of which grow predominately or exclusively on serpentine in Greece, and the karyotype morphology is illustrated in all cases but one. Chromosome data are provided for the first time for ten taxa (*Alyssum pogonocarpum*, *Centaurea charrellii*, *C. vlachorum*, *Cephalaria fanourii*, *Matricaria tempskyana*, *Onosma stridii*, *Scorzonera doriae*, *Silene fabarioides*, *S. solamandra*, *Trinia glauca* ssp. *pindica*) and for the endemic monospecific genus *Leptoplax*. A new number is reported for *Thymus teucroides* SSP. *candilicus*. An unexpected dysploid number is recorded for a population of *Leontodon hispidus* ssp. *hispidus*. Chromosome number and karyotype details from Greek populations are presented for the rest of the taxa. Chromosomal evidence supports close relationships among members of *Onosma* subsect. *Asterotricha*. The unusual chromosome number of *Centaurea vlachorum* supports its placement either in *C. sect. Jacea* or *C. sect. Cyanus*. The evolution of taxa in sections *Vierhapperia*, *Pulvinares*, and *Nervosae* of *Scorzonera* appears to be connected with particular chromosomal rearrangements and dysploidy. *Leptoplax* does not share the same chromosome number with *Peltaria* but with *Bornmuellera* instead, something that facilitates infrageneric hybridization. Further issues of taxonomy, distribution, evolution and conservation of serpentine species are briefly discussed where appropriate. (C) 2002 The Linnean Society of London.

- Cotrim, H. C., M. W. Chase, et al. (2003). "*Silene rothmaleri* P. Silva (Caryophyllaceae), a rare, fragmented but genetically diverse species." *Biodiversity and Conservation* 12(6): 1083-1098.
 conservation biology; gene flow; genetic diversity; DNA; *Silene*; Caryophyllaceae; endemism; Portugal; Europe; fragmentation
Silene rothmaleri is an endemic Portuguese species considered extinct until 1992, when it was rediscovered in the wild with a highly fragmented distribution. These rare plants occur along the southwestern Portuguese coast in small populations, which in addition to phenological differences that occur along the north-south gradient could create a pattern of genetic isolation. To evaluate the degree of genetic diversity and estimate the relationship between population fragmentation and genetic variability, we analysed the five known populations of *S. rothmaleri* using random amplified polymorphic DNA. Degree of polymorphism and Shannon Index of phenotypic diversity revealed high levels of diversity, found mainly within populations. PCo and cluster analysis revealed a distinct north-south cline, which was confirmed by spatial autocorrelation (Mantel) analysis. This indicates the existence of gene flow between small nearby populations and its insufficiency between widely separated populations. Levels of gene flow (Nm) estimated from the Shannon Index reveal a pattern consistent with a larger past distribution that went through a period of contraction and lack of gene flow followed by population differentiation. The central and largest population probably acts as a core of genetic variability inherited as a relict from a larger and more diverse ancestral population.
- Damboldt, J. and D. Phitos (1966). "Ein Beitrag zur Zytotaxonomie der Gattung *Silene* L. in Griechenland." *Österreichische Botanische Zeitschrift* 118: 169-175.
 TW; molecular biology; systematics; taxonomy; *Silene*; Caryophyllaceae; Greece; Europe; mediterranean
- Damboldt, J. and D. Phitos (1970). "Beiträge zur Flora Ionica. II. Bemerkungen zu einigen *Silene*-Arten aus Griechenland." *Österreichische Botanische Zeitschrift* 118: 341-352.
 TW; Greece; Flora; Europe; mediterranean; *Silene*; Caryophyllaceae; systematics; taxonomy;
- Delmotte, F., E. Bucheli, et al. (1999). "Host and parasite population structure in a natural plant-pathogen system." *Heredity* 82: 300-308.
 TW; parasitism; Caryophyllaceae; *Silene*; Ustilaginales; gene flow; mating system; reproduction; pollination
- Delph, L. F. (2004). "Testing for sex differences in biparental inbreeding and its consequences in a gynodioecious species." *American Journal of Botany* 91(1): 45-51.
 TW; *Silene*; Caryophyllaceae; sex; polymorphism; inbreeding depression; artificial pollination; xenogamy; breeding system
- Delph, L. F., M. F. Bailey, et al. (1999). "Seed provisioning in gynodioecious *Silene acaulis* (Caryophyllaceae)." *American Journal of Botany* 86(1): 140-144.
 TW; Caryophyllaceae; embryo; biomass; fruit set; gynodioecy; *Silene*; pollination; gynodioecy; hermaphrodite; reproduction; seed set
 In gynodioecious species, which contain females and hermaphrodites, the outcrossed seeds of females have been found to outperform the outcrossed seeds of hermaphrodites, in spite of the fact that their seeds are not larger in mass. Females do not make pollen. Hence the nutrients that hermaphrodites allocate to pollen, such as nitrogen, might be allocated to seeds by the females, such that individual seeds from females are better provisioned than those from hermaphrodites. Alternatively, females might make more seeds, rather than better provisioned seeds. We tested the hypothesis that seeds from females would be better provisioned for the gynodioecious species *Silene acaulis*, by comparing seed mass, embryo/endosperm mass, nitrogen and phosphorus content, and energy content for outcrossed seeds from females and hermaphrodites produced in a natural population. We also measured the proportion of flowers that set fruit in both morphs. Seeds from the two sexual morphs were not found to differ significantly for any of the measures of seed provisioning, with seeds from females containing either nonsignificantly less or equivalent amounts of each of the measures as compared to hermaphrodites. However, females set a significantly higher proportion of their flowers to fruit, as compared to hermaphrodites. These results indicate that females do not provision individual seeds more than hermaphrodites in *S. acaulis*, and alternative hypotheses will need to be examined to explain the difference in the performance of the seeds from the two sexual morphs.

- Delph, L. F. and S. B. Carroll (2001). "Factors affecting relative seed fitness and female frequency in a gynodioecious species, *Silene acaulis*." *Evolutionary Ecology Research* 3(4): 487-505.
gynodioecy; sex ratio; Caryophyllaceae; breeding system; dimorphism
Sex-ratio variation is common among gynodioecious species. One argument predicts that when sex is determined by a combination of nuclear and cytoplasmic factors, the frequency of females will be determined by genetic rather than ecological factors. An alternative argument suggests that the relative seed fitness of the female and hermaphroditic morphs will control female frequency. Hence, sex-ratio variation can be influenced by any factor that affects relative seed fitness, including ecological factors such as variation in pollination or site quality. In this study, we investigated sex-ratio variation in the gynodioecious species *Silene acaulis*, which has nuclear-cytoplasmic sex determination. We determined whether the frequency of females in 10 sites on Niwot Ridge, in the Front Range of Colorado, was correlated with the quality of the site or the relative seed fitness of the two morphs. Furthermore, we determined whether the two morphs differed consistently in investment in flowers, ovules, seeds and fruits. We found significant variation in sex ratio, site quality and relative seed fitness of the two morphs across sites. Although ovule number was greater in flowers on females, seed number per fruit did not vary in a consistent manner between morphs. The morphs differed consistently only in their propensity to produce fruit, with hermaphrodites exhibiting highly variable, and relatively low, fruit set compared to females. Female frequency was not significantly correlated with site quality. However, the relative seed fitness of the morphs was significantly correlated with site quality and the frequency of females. These results suggest that ecological factors do play a role in determining female frequency in *S. acaulis* and, consequently, can impact breeding-system evolution in this long-lived species.
- Delph, L. F., M. H. Johannsson, et al. (1997). "How environmental factors affect pollen performance. Ecological and evolutionary perspectives." *Ecology* 78(6): 1632-1639.
TW; EM; Cucurbita; Lobelia; *Silene*; ecology; herbivory; pollen; competition; genotype
We review the effects of herbivory and other environmental factors on pollen performance in plants. We conclude that natural levels of variation in herbivory and other environmental factors during pollen development are often sufficient to cause significant differences in pollen performance, and that the differences in pollen performance are likely to be caused by differences in the provisioning of pollen grains. From an evolutionary perspective, we discuss how pollen and ovule provisioning may be negatively genetically correlated and how this would maintain genetic variation for pollen performance within populations. Furthermore, the highly plastic nature of pollen performance provides the potential for genotypes to respond differently to environmental variation (genotype-environment interactions), which would also promote the maintenance of genetic variation in pollen performance.
- Delph, L. F., F. N. Knapczyk, et al. (2002). "Among-population variation and correlations in sexually dimorphic traits of *Silene latifolia*." *Journal of Evolutionary Biology* 15(6): 1011-1020.
experiment; dioecy; resource allocation; dimorphism; selection; *Silene*; population; sex;
The degree of sexual dimorphism in a trait may be determined directly by disruptive selection, as well as by correlations with other traits under selection. We grew seeds from nine populations of the dioecious plant *Silene latifolia* in a common-garden experiment to determine whether phenotypic variation and correlations existed for floral, leaf and resource allocation traits, and whether this variation had a genetic component. We also determined the traits which were sexually dimorphic, the degree of dimorphism, and whether it varied among populations. Seven traits exhibited among-population variation and sexual dimorphism. Variation in the degree of dimorphism occurred only for two traits, suggesting that dimorphism may be evolving more slowly than trait means. Males had more, smaller flowers, shorter leaves, and allocated less of their total biomass to stems and more to leaves than females. Flower production was the most sexually dimorphic trait and was correlated with all measured traits. Most traits exhibited significant correlations between the sexes. The pattern of correlations and the degree of sexual dimorphism among traits lead us to suggest that intrasexual selection for an exaggerated floral display in males has indirectly led to sexual dimorphism in a host of other traits.
- Delph, L. F., F. N. Knapczyk, et al. (2003). "Among-population variation and correlations in sexually dimorphic traits of *Silene latifolia* (vol 15, pg 1011, 2002)." *Journal of Evolutionary Biology* 16(1): 177-177.
Silene; Caryophyllaceae; population; sex; dimorphism; morphology
- Delph, L. F. and T. R. Meagher (1995). "Sexual dimorphism masks life-history trade-offs in the dioecious plant *Silene latifolia*." *Ecology* 76(3): 775-785.

dioecy; *Silene*; Caryophyllaceae; life history; costs; reproduction; growth; fruit set
Females of dioecious plant species are expected to show greater trade-offs with other life history traits than males because of their high investment in reproduction. We investigated life history traits and resource allocation patterns for both males and females of the dioecious plant *Silene latifolia*, to document allocation both prior to and after reproductive investment. In addition, the impact of fruit production on subsequent allocation to reproduction and growth was investigated by varying the number of flowers pollinated females. The mean date of first reproduction was the same for males and females. Early-flowering plants of both sexes invested less in leaf biomass than plants that delayed flowering. The percentage of flowers pollinated had a significant effect on how resources were allocated, and on the amount and timing of further flower production. Sexual dimorphism was observed in resource allocation patterns after, but not prior to, investment in reproduction. Overall, pollinated females were found to have more leaf biomass and invest nearly twice as much in reproduction as males, in spite of an apparent trade-off between leaf production and reproduction within both females and males. We conclude that sexual dimorphism in life history traits that affects resource acquisition causes the resource pool that is allocated to be variable, rather than static, thereby masking the underlying tradeoffs.

- Delph, L. F. and P. Mutikainen (2003). "Testing why the sex of the maternal parent affects seedling survival in a gynodioecious species." *Evolution* 57(2): 231-239.
fitness; selection; gynodioecy; seed; size; *Silene*; Caryophyllaceae; seedling; recruitment; fitness;
In gynodioecious plants, seed offspring from hermaphrodites often perform less well than those from females. This lower performance sometimes can be attributed to inbreeding by hermaphrodites or to relatively greater provisioning of individual seeds by females. However, these hypotheses are not explanatory when only outcrossing occurs and when individual seeds of the two morphs are equally well provisioned. Three hypotheses may explain the lower fitness of seed offspring from hermaphrodites in such cases. The morphology hypothesis states that the opportunity for gametophytic selection is lower within flowers of hermaphrodites compared to flowers on females, because the perfect flowers of hermaphrodites are relatively short-styled. The cytotype hypothesis states that the performance difference is directly caused by an individual's cytotype, whose frequency in the population may differ for the two sex morphs. The pleiotropy hypothesis states that negative pleiotropic effects of nuclear restorer alleles or alleles hitchhiking with them are expressed more often by offspring from hermaphrodites. We performed two experiments using the gynodioecious plant *Silene acaulis* to contrast these hypotheses. In our first experiment we contrasted the morphology and pleiotropy hypotheses by performing controlled pollinations and subsequently planting seeds in both the greenhouse and field. Hermaphrodites of *S. acaulis* can produce both pistillate and perfect flowers, which allowed us to determine whether flower morphology affects offspring survivorship independent of the sex of the maternal parent. We found that neither seed mass nor germination differed between seeds from females and hermaphrodites. Offspring from pistillate flowers on hermaphrodites did not differ significantly in their survival compared to offspring from perfect flowers on hermaphrodites, but had lower survivorship compared to offspring from pistillate flowers on females, refuting the morphology hypothesis. In a second experiment, we compared offspring survival of full-sibling pairs of females and hermaphrodites (who shared the same cytoplasm) to contrast the cytotype and pleiotropy hypotheses. We found that seed offspring from females and hermaphrodites that shared the same cytoplasm differed in their survival, which is counter to the prediction of the cytotype hypothesis. In both experiments, the sex of the maternal parent significantly affected offspring survival, with seed offspring from hermaphrodites surviving less well than those from females. These results support the pleiotropy hypothesis. We conclude by discussing alternative ways of thinking about negative pleiotropic effects of nuclear restorers or "the cost of restoration."
- Delph, L. F., C. Weinig, et al. (1998). "Why fast-growing pollen tubes give rise to vigorous progeny the test of a new mechanism." *Proceedings of the Royal Society of London B* 265: 935-939.
TW; EM; pollen; pollen stigma interaction; competition; growth; maternal effects; *Silene*;
Caryophyllaceae
- Desfeux, C. and D. Lejeune (1996). "Systematics of euromediterranean *Silene* (Caryophyllaceae) evidence from phylogenetic analysis using ITS sequences." *Comptes Rendus de L'Academie Des Sciences Serie III - Sciences de La Vie - Life Sciences* 319: 351-358.
TW; molecular biology; evolution; genetics; Caryophyllaceae; *Silene*; mediterranean; Europe;
systematics; taxonomy; methods

- Desfeux, C., S. Maurice, et al. (1996). "Evolution of reproductive systems in the genus *Silene*." Proceedings of the Royal Society of London B 263: 409-414.
TW; evolution; reproduction; *Silene*; Caryophyllaceae; systematics; taxonomy; breeding system; pollination; EM
- Deutsch, A. "Bestimmungsschlüssel für Grünlandpflanzen."
TW; Germany; key; *Silene*; Caryophyllaceae
- Dolan, R. W. (1994). "Patterns of isozyme variation in relation to population size, isolation, and phytogeographic history in royal catchfly (*Silene regia*; Caryophyllaceae)." American Journal of Botany 81: 965-972.
TW; allozyme; demography; isolation; genetics; biogeography; *Silene*; Caryophyllaceae; systematics; taxonomy; evolution;
The distribution of genetic variation within and among plant populations is influenced by both contemporary and historical factors. I used isozyme analysis of band phenotypes to examine genetic structure in the rare prairie forb *Silene regia*. Relationships between current-day population size, isolation, and phenotypic variation were assessed for 18 populations in two regions with differing postglacial history. Western populations from unglaciated southern Missouri and Arkansas were more genetically diverse based on the Shannon-Weaver index (H) and a polymorphic index than were more eastern populations. These differences may be due to loss of variation with repeated founding of new populations in previously glaciated sites in Indiana and Ohio. Within the western region, population size was not significantly correlated with genetic variation. In the east, size was correlated with Shannon-Weaver diversity. There was no relationship between variation and isolation in either region, but eastern populations were slightly more differentiated. Greater among-population differentiation and the demonstrated connection between population size and variation in the eastern sites may reflect lower levels of interpopulation gene flow in the fragmented remnant prairies of Indiana and Ohio.
- Donnison, I. S. and D. Francis (2002). "Models of floral pattern in detached flowers of *Silene coeli-rosa* (L.) Godr. (Caryophyllaceae)." Botanical Journal of the Linnean Society 140(3): 229-235.
Silene; flower development; Caryophyllaceae; flower; morphology; physiology
Organ number per whorl was analysed in aberrant flowers of the long-day (LD) plant, *Silene coeli-rosa*, to test a hypothesis that organ number in a whorl takes its cue from an adjacent outer whorl and that perturbed organ number per whorl is not random but defaults to that of closely related taxa or genera of the Caryophyllaceae. When plants were grown under short-days (SD), transferred to LD and the shoot meristem excised and cultured in vitro under SD, the normal pattern of flower development was often disrupted. For example, we observed flowers which comprised floral whorls with an aberrant number of floral organs. In part, this was an effect of tissue culture; however, the over-and-above effect was the establishment of an alternative pattern of development. Our data indicate that two distinct and recurrent patterns occurred in the aberrant flowers we observed in five separate experiments. First, pairs of floral whorls were linked so that aberration in one whorl resulted in the next whorl being more aberrant than normal. Second, the number of organs in aberrant whorls was not random, but defaulted to an organ number which mimicked the flowers of closely related species of *Silene* or related genera in the Caryophyllaceae. (C) 2002 The Linnean Society of London
- Dudash, M. R. and C. B. Fenster (1997). "Multiyear study of pollen limitation and cost of reproduction in the iteroparous *Silene virginica*." Ecology 78(2): 484-493.
Silene; Caryophyllaceae; pollen limitation; ornithophily; pollination; North America; costs; reproduction; success
We investigated whether pollen deposited onto stigmas limited female reproductive success in the hummingbird-pollinated, short-lived, iteroparous, *Silene virginica* (Caryophyllaceae). The study was conducted over a 4-yr span in a population occurring in a woodland area and over a 3-yr span in a second population occurring in a nearby open meadow. We contrasted average fruit set, seed set per fruit, and total annual seed production (in only the woodland site) between open-pollinated control plants and hand-pollinated experimental plants. We also followed surviving individuals in subsequent years and repeated the same treatments on plants when they flowered. All plants were monitored annually for survival and reproduction at both sites; growth was monitored at only the woodland site because of extensive herbivory in the meadow population. Lack of pollen deposited onto stigmas significantly limited reproductive potential at the level of percentage fruit set throughout the study for both sites. In contrast, pollen deposition onto stigmas exhibited considerable site and year heterogeneity in its effect on seed production per fruit. In the cumulative test of pollen limitation,

however, we detected no difference between total annual seed production between our open-pollinated control and hand-pollinated experimental plants in the woodland site during the 4-yr study. A weak negative trend was detected between fruit set per plant and average seed set per fruit among all plants in the woodland site, suggesting a limited role for an intraplant compensation mechanism. No significant trade-off was detected in probability of survival and flowering between the control and hand-pollinated experimental treatment groups at either site. In addition, no cost was detected in future growth and reproduction in the woodland population. Similar total seed production among individuals in the two treatment groups explains in part, why no difference was observed in future survival, growth, and reproduction between the control and hand-pollinated treatment groups.

Dudash, M. R. and C. B. Fenster (2001). "The role of breeding system and inbreeding depression in the maintenance of an outcrossing mating strategy in *Silene virginica* (Caryophyllaceae)." *American Journal of Botany* 88(11): 1953-1959.

TW; breeding system; Caryophyllaceae; geitonogamy; ornithophily; inbreeding depression; mating system; *Silene*; pollen limitation; artificial pollination; progeny vigor; xenogamy; evolution; reproduction

The goal of this study was to understand the interaction among breeding system, mating system, and expression of inbreeding depression in the hermaphroditic, primarily hummingbird-pollinated, iteroparous, short-lived perennial *Silene virginica*. We performed hand-selfed and hand-outcrossed pollinations in the field, conducted detailed floral observations within individual flowers and plants, and assayed adult tissue from flowering plants for a genetic estimate of population xenogamy rate. We quantified the opportunity for geitonogamy as the proportion of days each plant exhibited simultaneous male and female function, i.e., asynchronous expression of male- and female-phased flowers. Expression of cumulative inbreeding depression based on germination rate and total flower production in the glasshouse was similar to 40% and was congruent with the estimated high outcrossing rate of 0.89. Floral observations demonstrated strong temporal protandry within each flower (dichogamy) as well as complete spatial separation between male and female function within each flower (herkogamy). On average, 29% of the time there were both male- and female-phased flowers present on an individual plant. We conclude that our estimate of inbreeding depression is compatible with a largely xenogamy mating system and the amount of selfing observed, likely results from geitonogamy. This study illustrates the utility of examining both the causes and the consequences of inbreeding via selfing to provide additional insights into the evolution of plant mating systems.

Dufay, M. and M. C. Anstett (2003). "Conflicts between plants and pollinators that reproduce within inflorescences: evolutionary variations on a theme." *Oikos* 100(1): 3-14.

TW; mutualism; interaction; pollination; parasitism; evolution; coevolution; deceit; competition; interaction; *Silene*; Caryophyllaceae; *Yucca* moth; predation; seed; flower

The high diversity of mutualisms has probably limited the development of a general theory about their evolution and their stability. Here we review conflicts of interests occurring in the 13 known nursery pollination systems, where pollinators reproduce within the inflorescence they pollinate. We found three main conflicts of interest between mutualists that correspond to the following evolutionary questions: 1) Why do plants not kill their pollinators' larvae? 2) Why do pollinators visit deceptive flowers? and 3) Why do pollinators pollinate? We show that the reproductive system of the plant is strongly correlated not only with the set of conflicts of interests that actually occur but also with the proximal resolution of these conflicts. In many cases the evolutionary stability of nursery pollination mutualisms relies on the avoidance of intra-specific competition among pollinator larvae. This stabilizing factor could perhaps also explain the absence of overexploitation in other mutualisms.

Dulberger, R. and A. Horovitz (1984). "Gender polymorphism in flowers of *Silene vulgaris* (Moench) Garcke (Caryophyllaceae)." *Botanical Journal of the Linnean Society* 89: 101-117.

TW; polymorphism; *Silene*; Caryophyllaceae; Israel; polyploidy; hermaphrodite; gynomonoeicy; pollen stigma interaction; EM; literature;

Elmqvist, T., D. Liu, et al. (1993). "Anther-smut infection in *Silene dioica*: Variation in floral morphology and patterns of spore deposition." *Oikos* 68(2): 207-216.

Mycophyta; Ustilaginales; *Silene*; Caryophyllaceae; flower; morphology; TW; parasitism
The anther-smut *Microbotryum violaceum*, causes a systemic perennial infection of its host *Silene dioica*. Infection results in sterility and the production of teliospores in flowers. These spores are transmitted to healthy plants by flower visiting insects. The behavioural responses of flower visiting insects to a variation in floral characters are therefore likely to affect rates of pollen export/import,

the rate of spore deposition and probability of disease. Since infected plants are sterilized, they are effectively removed from the gene pool. It is therefore often assumed that in this host-pathogen system there is a considerable potential for a pathogen-pollinator mediated selection on floral characters. In a transplantation experiment, which included plants from four different populations, we tested for correlations between variation in female floral morphology and patterns of spore and pollen deposition, and a resulting risk of disease. The source populations in this experiment were located on four islands in Skeppsvik archipelago in northern Sweden, and represented a gradient of disease incidence from completely healthy (Island 1), low incidence (Island 2) to high incidences (Islands 3 and 4) of disease. Fifty plants from each population were transplanted to the centre of the population on Island 4. Plants from the non-diseased population had larger flowers and longer styles than plants from the highly diseased populations. Numbers of pollen grains and spores deposited on flowers were strongly and positively correlated. We found that plants originating from the healthy population received approximately four times more pollen and nine times more spores per flower than the individuals from the resident diseased population. The resulting incidences of disease among plants from the four Populations differed significantly, and was 20% among plants originating from the healthy population and 0% among plants from the resident highly diseased population. Plants from the other two diseased populations showed intermediate values (13% and 11% respectively). In a survey of ten populations we found among healthy plants a significant negative correlation between mean style length (positively correlated with corolla size and ovule number) and incidence of disease. The potential for pathogen-pollinator mediated selection on floral characters in this host-pathogen system is discussed.

Emery, S. N. and D. E. McCauley (2002). "Consequences of inbreeding for offspring fitness and gender in *Silene vulgaris*, a gynodioecious plant." *Journal of Evolutionary Biology* 15(6): 1057-1066.
gynodioecy; inbreeding depression; *Silene*; sex; Caryophyllaceae; population; inbreeding; gynodioecy; breeding system; fitness

In gynodioecious plants, hermaphrodite and female plants co-occur in the same population. In these systems gender typically depends on whether a maternally inherited cytoplasmic male sterility factor (CMS) is counteracted by nuclear restorer alleles. These restorer alleles are often genetically dominant. Although plants of the female morph are obligatorily outcrossing, hermaphrodites may self. This selfing increases homozygosity and may thus have two effects: (1) it may decrease fitness (i.e. result in inbreeding depression) and (ii) it may increase homozygosity of the nuclear restorer alleles and therefore increase the production of females. This, in turn, enhances outcrossing in the following generation. In order to test the latter hypothesis, experimental crosses were conducted using individuals derived from four natural populations of *Silene vulgaris*, a gynodioecious plant. Treatments included self-fertilization of hermaphrodites, outcrossing of hermaphrodites and females using pollen derived from the same source population as the pollen recipients, and outcrossing hermaphrodites and females using pollen derived from different source populations. Offspring were scored for seed germination, survivorship to flowering and gender. The products of self-fertilization had reduced survivorship at both life stages when compared with the offspring of outcrossed hermaphrodites or females. In one population the fitness of offspring produced by within-population outcrossing of females was significantly less than the fitness of offspring produced by crossing females with hermaphrodites from other populations. Self-fertilization of hermaphrodites produced a smaller proportion of hermaphroditic offspring than did outcrossing hermaphrodites. Outcrossing females within populations produced a smaller proportion of hermaphrodite offspring than did crossing females with hermaphrodites from other populations. These results are consistent with a cytonuclear system of sex determination with dominant nuclear restorers, and are discussed with regard to how the mating system and the genetics of sex determination interact to influence the evolution of inbreeding depression.

Erwin, J. E. and R. M. Warner (2002). Determination of photoperiodic response group and effect of supplemental irradiance on flowering of several bedding plant species. In, *Proceedings of the Fourth International IShs Symposium on Artificial Lightings*. Leuven 1, International Society Horticultural Science: 95-99.

photoperiodism; fastcropping; *Ageratum houstonianum*; *Anethum graveolens*; *Antirrhinum majus*; *Calendula officinalis*; *Celosia plumosa*; *Convolvulus tricolor*; *Cleome hasslerana*; *Cosmos bipinnatus*; *Dianthus chinensis*; *Dimorphotheca pluvalis*; *Gazania rigens*; *Gomphrena globosa*; *Helipterum roseum*; *Lavatera trimestris*; *Limnanthes douglasii*; *Limonium sinuatum*; *Linaria maroccana*; *Lobelia erinus*; *Mimulus x hybridus*; *Mirabilis jalapa*; *Nemophila maculata*; *Nicotiana alata*; *Nigella damascena*; *Origanum vulgare*; *Papaver rhoes*; *Salvia splendens*; *Silene armeria*; *Zinnia elegans*

Flower induction of many plant species is synchronized temporally during the year by utilizing changes in day or night length. Commercial potted plant growers have used photoperiod manipulation to induce flowering of short-day plants on a year round basis. A lack of application of photoperiod to manipulate growth of current spring annuals has, in part, been due to the lack of information identifying the photoperiodic classifications of each species. This paper outlines a series of experiments that identified the photoperiodic group classifications and responses to supplemental irradiance of 28 spring annual species. No species studied were identified as obligate short-day plants. Most species were either obligate or facultative long-day plants. Species in which growers have traditionally had difficulty in producing marketable flowering plants in spring tended to be obligate long-day plants. In contrast, a number of species that tend to flower later in the season than desirable were identified as facultative short-day plants. In addition, species varied in their flowering response to supplemental lighting treatments. Leaf number below the first flower was affected by the addition of supplemental lighting under inductive conditions with approximately one half of the species studied.

Farbos, I., J. Veuskens, et al. (1999). "Sexual dimorphism in white campion: Deletion on the Y chromosome results in a floral asexual phenotype." *Genetics* 151(3): 1187-1196.

TW; dioecy; *Silene*; sex ;dimorphism; DNA; expression; evolution; genetics; morphology; Caryophyllaceae; molecular biology; karyosystematics; phenotype; flower; morphology
White campion is a dioecious plant with heteromorphic X and Y sex chromosomes. In male plants, a filamentous structure replaces the pistil, while in female plants the stamens degenerate early in newer development. Asexual (asx) mutants, cumulating the two developmental defects that characterize the sexual dimorphism in this species, were produced by gamma ray irradiation of pollen and screening in the M-1 generation. The mutants harbor a novel type of mutation affecting an early function in sporogenous/parietal cell differentiation within the anther. The function is called stamen-promoting function (SPF). The mutants are shown to result from interstitial deletions on the Y chromosome. We present evidence that such deletions tentatively cover the central domain on the (p)-arm of the Y chromosome (Y2 region). By comparing stamen development in wild-type female and asx mutant flowers we show that they share the same block in anther development, which results in the production of vestigial anthers. The data suggest that the SPF, a key function (s) controlling the sporogenous/parietal specialization in premeiotic anthers, is genuinely missing in females (XX constitution). We argue that this is the earliest function in the male program that is Y-linked and is likely responsible for "male dimorphism" (sexual dimorphism in the third floral whorl) in white campion. More generally, the reported results improve our knowledge of the structural and functional organization of the Y chromosome and favor the view that sex determination in this species results primarily from a trigger signal on the Y chromosome (Y1 region) that suppresses female development. The default state is therefore thf ancestral hermaphroditic state.

Fenster, C. B. and D. E. Carr (1997). "Genetics of sex allocation in *Mimulus* (Scrophulariaceae)." *Journal of Evolutionary Biology* 10(4): 641-661.

Silene; Caryophyllaceae; evolution; resource allocation; sex; dioecy; P/O
Theoretical models of the evolution of resource allocation patterns to male and female function make the assumption that there are inherent trade-offs between the two. Here we use a quantitative genetic approach to quantify trade-offs between male and female function and to determine whether plant populations could readily respond to natural selection by quantifying the amount of genetic variation for pollen and ovule production. Both intra-and interspecific crossing designs were applied to two populations of the predominantly outcrossing *Mimulus guttatus* and two populations of the highly selfing congener, *M. micranthus*. The only significant correlations observed among pollen number, pollen size and ovule number were positive. Positive genetic correlations among the traits were sometimes reduced after removing the effect of flower size but still no significant negative correlations were detected. These results suggest that positive correlations between pollen and ovule production may be due to the joint positive correlation of these characters with the resource pool available for pollen and ovule production, as reflected by flower size. Heritabilities were moderate to high for ovule production but low for pollen number and pollen size and suggest that responses to selection would differ between the two traits. Crosses between the species revealed that there are additional genetic factors contributing to differences between the two species for corolla width, vs. pollen:ovule ratio. This is consistent with the hypothesis that genetic variation for resource acquisition may in part be responsible for the overall lack of a negative correlation between pollen and ovule production and provides a genetic explanation for little evidence of trade-offs between sexual functions in *Mimulus*.

Fenster, C. B. and M. R. Dudash (2001). "Spatiotemporal variation in the role of hummingbirds as pollinators of *Silene virginica*." *Ecology* 82(3): 844-851.

TW; Trochilidae; interaction; pollination; pollination syndromes; *Silene*; Caryophyllaceae; Ornithophily; melittophily; North America; efficiency; success

Pollination restricted to a guild of visitors is central to the concept of pollination syndromes. However, there is limited quantitative evidence that the pollination of plants exhibiting certain pollination syndromes is actually dominated by the expected guild of pollinators. We determined the importance of the sole hummingbird species in eastern North America, the Ruby-throat, *Archilochus colubris*, and invertebrate visitors as pollinators of *Silene virginica*, which exhibits traits commonly associated with hummingbird pollination. We quantified the role of either type of visitor as pollinators by comparing female reproductive success of plants that were allowed free access by all visitors to female reproductive success of caged plants that were restricted to pollination by invertebrates (small bees and flies, and in one year *Bombus* spp.). Spatial and temporal variation in the role of either type of pollinator was documented by comparing the female reproductive success of caged and control plants in two nearby sites for five years. In general we found that hummingbirds are the predominant pollinator of *S. virginica*, but there is considerable spatiotemporal variation in their role. We discuss the importance of understanding the role of hummingbirds as potential selective agents of *S. virginica* floral traits within the greater community context of other potential pollinators.

Fenster, C. B., C. L. Hassler, et al. (1996). "Fluorescent dye particles are good pollen analogs for hummingbird-pollinated *Silene virginica* (Caryophyllaceae)." *Canadian Journal of Botany* 74: 189-193.

Caryophyllaceae; TW; methods; Ornithophily; *Silene*; pollen; gene flow

We tested the utility of fluorescent dye particles as pollen analogs for hummingbird-pollinated *Silene virginica*, (Caryophyllaceae) by comparing the movement of pollen and fluorescent dye across sequentially visited emasculated flowers. We found no differences in either the intercept or the slope of the regressions of the two particle types on floral visitation sequence. In addition, the presence of fluorescent powder on the stigmas of a flower was a good indicator of pollen transferred to that flower. Both pollen and dye particles were transported almost identical distances in the flower sequence. These data indicate that fluorescent powder is a good pollen analog for *S. virginica*. We compare our findings with previous studies examining the utility of fluorescent dye as a pollen analog.

Ferrazzi, P. (1988). "*Silene*." *Apicoltore Moderno* 79(2): 79-82.

The several species of *Silene* genus are characterized by a long and narrow corolla. This shape makes hard the harvesting of the nectar, that is produced in the bottom of the flower at the staminal base. Nevertheless, *Apis mellifera* L. manages to suck the nectar pushing-like in *S. vulgaris* (Moench) Garcke-into the corolla. For pollen, the honeybees lean on the outside of the flowers. The night-blooming *Silenes* are prevalingly pollinated by Noctuid and Sphingid moths. The apicultural significance of this genus is low. The apolar and periporate *Silene* pollen grains are seldom found in the honeys.

Filatov, D. A., F. Moneger, et al. (2000). "Low variability in a Y-linked plant gene and its implications for Y-chromosome evolution." *Nature* 404(6776): 388-390.

Sex chromosomes have evolved independently in several different groups of organisms, but they share common features, including genetic degeneration of the Y chromosome(1,2). Suppression of recombination between ancestral proto-X and proto-Y chromosomes is thought to have led to their gradual divergence, and to degeneration of the Y chromosome(2), but the evolutionary forces responsible are unknown. In non-recombining Y chromosomes, deleterious mutations may be carried to fixation by linked advantageous mutations ("selective sweeps")(3). Occurrence of deleterious mutations may drive "Muller's ratchet" (stochastic loss of chromosomes with the fewest mutations)(2,4). Selective elimination of deleterious mutations, causing "background selection"(5,6) may accelerate stochastic fixation of mildly detrimental mutations(2). All these processes lower effective population sizes, and therefore reduce variability of genes in evolving Y chromosomes. We have studied DNA diversity and divergence in a recently described X- and Y-linked gene pair(7) (SLX-1 and SLY-1) of the plant *Silene latifolia* to obtain evidence about the early stages of Y degeneration. Here we show that DNA polymorphism in SLY-1 is 20-fold lower than in SLX-1, but the pattern of polymorphism does not suggest a selective sweep.

Frick, B. and P. B. Cavers (1989). "Aberrations in sex expression in *Silene latifolia*." *American Naturalist* 134: 562-573.

sexual system; sex; *Silene*; Caryophyllaceae; dioecy; hermaphrodite; SB; TW

- Galeuchet, D. J., R. Husi, et al. (2002). "Characterization of microsatellite loci in *Lychnis flos-cuculi* (Caryophyllaceae)." *Molecular Ecology Notes* 2(4): 491-492.
Caryophyllaceae; habitat; fragmentation; *Lychnis*; primers; *Silene*; Switzerland; molecular biology; DNA; genetics
We cloned microsatellite repeats from ragged robin *Lychnis flos-cuculi* (Caryophyllaceae) and developed 20 primer pairs for microsatellite marker analysis. We used 18 individuals of a large Swiss population to screen microsatellites. Seven loci were polymorphic. Between seven and 11 alleles were found per locus and the observed heterozygosity was between 0.308 and 0.813. Observed heterozygote deficits were significant in five of the seven loci, in line with the mixed mating system of *L. flos-cuculi*.
- Gardener, M. C. and M. P. Gillman (2001). "Analyzing variability in nectar amino acids: composition is less variable than concentration." *Journal of Chemical Ecology* 27(12): 2545-2558.
TW; nectar; amino acid; HPLC; variation; compounds; *Silene*; *Agrostemma*; Caryophyllaceae; *Lychnis*; Epilobium; Onagraceae; Lamiaceae; Fabaceae; Primulaceae; Caprifoliaceae; Convolvulaceae; Rubiaceae; Asteraceae; Boraginaceae; Apocynaceae
Thirty species of flowering plants were analyzed for floral nectar amino acid composition. High-performance liquid chromatography (HPLC) was used in conjunction with AccQtag derivatization to produce accurate and precise data. For any one species, the total concentration of amino acids varies greatly (average coefficient of variation 0.65), but composition is much less variable (average correlation among samples from a single species 0.85). Absolute concentration of individual amino acids is much more variable than the relative abundance (coefficients of variation 0.98 and 0.77, respectively; N = 544, t = 16.98, P < 0.001). When amino acids that occur in only small relative abundance (<1%) are removed from the analysis, the difference is even more marked (0.78 and 0.51, respectively; N = 344, t = 15.13, P < 0.001). The results highlight the need for large sample sizes when making observations concerning the absolute amounts of amino acids in nectar and for sensitive analyses of the composition, as even small changes may be biologically significant.
- Gehring, J. L. (1993). "Temporal patterns in the development of sexual dimorphisms in *Silene latifolia* (Caryophyllaceae)." *Bulletin of the Torrey Botanical Club* 120: 405-416.
Caryophyllaceae; polymorphism; breeding system; Blütenentwicklung; dioecy; pattern; sex; *Silene*; TW
- Gehring, J. L. and L. F. Delph (1999). "Fine-scale genetic structure and clinal variation in *Silene acaulis* despite high gene flow." *Heredity* 82: 628-637.
TW; Caryophyllaceae; *Silene*; gene flow; allozyme; genetics;
- Gehring, J. L. and Y. B. Linhart (1993). "Sexual dimorphisms and response to low resources in the dioecious plant *Silene latifolia* (Caryophyllaceae)." *International Journal of Plant Sciences* 154: 152-162.
dioecy; resource allocation; Geschlechtsdimorphismus; polymorphism; *Silene*; Caryophyllaceae; TW
- Gehring, J. L. and R. K. Monson (1994). "Sexual differences in gas exchange and response to environmental stress in dioecious *Silene latifolia* (Caryophyllaceae)." *American Journal of Botany* 81: 166-174.
physiology; Gaswechsel; Caryophyllaceae; dioecy; sex; *Silene*; TW
Females of dioecious species usually have higher reproductive effort than males because they produce fruits in addition to flowers. Since females have higher reproductive effort, they are expected to be more negatively affected than males by low resource availability. We tested that assumption by growing females and males of *Silene latifolia* under low levels of light, water, nitrogen, phosphorus, and potassium. Gas exchange of the sexes did not respond differently to low resource availability; higher female reproductive effort relative to males did not differentially affect their ability to assimilate carbon. However, male photosynthesis rates and stomatal conductances were slightly, but consistently, higher than those of females. The intersexual difference in photosynthesis rate may be a proximate result of reproduction if females translocate nutrients, particularly nitrogen, from their leaves to developing fruits. Alternatively (or perhaps additionally), higher male photosynthesis and stomatal conductances relative to females may be the ultimate result of sexual selection. This could be the case if 1) reproductive effort as estimated by biomass allocation is misleading and males actually invest more in reproduction than females, or 2) females experience stronger selection than males to conserve water late in the growing season, when soil moisture is likely to be low but females need to complete fruit maturation. Our results indicated that females had slightly lower leaf nitrogen but higher photosynthetic water-use efficiency than males,

so it is possible that both proximate and ultimate factors are operating simultaneously to cause lower female photosynthesis rates.

- Ghazanfar, S. A. (1984). "Pollenmorphology of the genus *Silene* L. (Caryophyllaceae), sections Siphonomorpha Otth. and Auriculatae (Boiss.) Schischk." *New Phytologist* 98: 683-690.
taxonomy; pollen; Caryophyllaceae; *Silene*; Palynologie; morphology; systematics; TW; SB
- Giles, B. E. and J. Goudet (1997). "Genetic differentiation in *Silene dioica* metapopulations. Estimation of spatiotemporal effects in a successional plant species." *American Naturalist* 149(3): 507-526.
TW; population; extinction; mathematical model; island; genetics; differentiation; Caryophyllales; Caryophyllaceae; *Silene*; Sweden; Scandinavia; Europe; demography; succession; ecology; SB
Silene dioica is a diploid, dioecious, perennial, insect-pollinated herb and part of the deciduous phase of primary succession in Skeppsvik Archipelago, Gulf of Bothnia, Sweden. These islands are composed of material deposited and left underwater by melting ice at the end of the last ice age. A rapid and relatively constant rate of land uplift of 0.9 cm per year continually creates new islands available for colonization by plants. Because the higher deposits appear first, islands differ in age. Because it is possible to estimate the ages of islands and populations of plant species belonging to early stages of succession, the genetic dynamics occurring within an age-structured metapopulation can be investigated in this archipelago. Fifty-two island populations of *S. dioica* of known ages, sizes, and distances from each other were studied through electrophoretic data. A number of factors increase the degree of genetic differentiation among these island populations relative to an island model at equilibrium. Newly founded populations were more differentiated than those of intermediate age, which suggests that colonization dynamics increase genetic variance among populations. The very old populations, which decrease in size as they approach extinction, were more differentiated than intermediate-aged populations. Isolation by distance occurs in this system. Colonizers are likely to come from more than one source, and the migrant pool model best explains colonization events in the archipelago. Degree of environmental exposure also affects population differentiation.
- Giles, B. E., E. Lundqvist, et al. (1998). "Restricted gene flow and subpopulation differentiation in *Silene dioica*." *Heredity* 80(Part 6): 715-723.
TW; gene flow; genetics; differentiation; population; distance; Coleoptera; model; SB;
Caryophyllaceae; *Silene*; gene flow; demography; dioecy; ecology; genetics; pollen; seed; dispersal; Isolation; Sweden; Skandinavia; Europe
The size of breeding units and the hierarchical population structure of the dioecious perennial herb *Silene dioica* were investigated on four closely situated island populations in the Skeppsvik Archipelago in northern Sweden. F-statistics analyses of nine polymorphic allozyme loci revealed that plants on single islands are divided into many small breeding units, between 0.2 m(2) and 6 m(2). Hierarchical analyses showed that levels of differentiation among subpopulations within islands (F-PL = 0.080) were about twice as high as among islands (F-LT = 0.048). These results are discussed in the light of what is known about pollen and seed movement in the archipelago.
- Giraud, T., E. Fournier, et al. (2002). "Isolation of 44 polymorphic microsatellite loci in three host races of the phytopathogenic fungus *Microbotryum violaceum*." *Molecular Ecology Notes* 2(2): 142-146.
Ustilaginales; pathogen; genetic diversity
We report the development of 44 microsatellite markers in three host races of the fungus *Microbotryum violaceum*, a sexually transmitted disease of the Caryophyllaceae. An enrichment protocol was used to isolate microsatellite loci from three strains, collected, respectively, from the plant species *Gypsophila repens*, *Dianthus sylvestris*, and *Silene vulgaris*. Polymorphism and cross-amplification were explored with 32 isolates of *M. violaceum*, collected on 12 different plant species in natural populations.
- Goulson, D. and K. Jerrim (1997). "Maintenance of the species boundary between *Silene dioica* and *S. latifolia* (red and white campion)." *Oikos* 79(1): 115-126.
The relative importance of floral versus ecological isolation in preventing hybridisation in plant species remains unknown, primarily due to a paucity of detailed data from a range of systems. We examined floral isolation between *Silene dioica* and *S. latifolia* (Caryophyllaceae) in southern England by measuring gene flow across the species boundary using allozymes, and by assessing interspecific transfer of fluorescent dye powders to simulate pollination. Allozyme studies of wild populations demonstrated that gene flow between *S. dioica* and *S. latifolia* is considerable since the two species could not be distinguished at the loci studied, in sharp contrast to their distinct morphologies. Pollination studies using fluorescent dye powders and direct observation of insect

behaviour concurred in that although there was a degree of assortative mating it was insufficient in itself to prevent introgression. Fluorescent dye studies also suggest that pollination rates of hybrids are similar to parental types and that they provide a bridge for gene flow since they are visited freely by the main pollinators of both *S. dioica* (bumblebees) and *S. latifolia* (moths). We conclude that although floral isolation and spatial segregation may be important contributory factors, morphological differences between species are probably maintained primarily by strong selective forces associated with habitat (ecological isolation).

- Grant, S., B. Hunkirchen, et al. (1994). "Developmental differences between male and female flowers in the dioecious plant *Silene latifolia*." *Plant Journal* 6: 471-480.
histology; sex determination
Caryophyllaceae; *Silene*; Geschlechtsdimorphismus; Blütenentwicklung; flower; morphology; SEM; dioecy; SB; TW
- Greuter, W. (1995). "*Silene* (Caryophyllaceae) in Greece a subgeneric and sectional classification." *Taxon* 44: 543-581.
taxonomy; systematics; Griechenland; *Silene*; Caryophyllaceae; evolution; EM; TW
- Greuter, W. (1995). "Studies in Greek Caryophylloideae *Agrostemma*, *Silene*, and *Vaccaria*." *Willdenowia* 25: 105-142.
systematics; Nomenklatur; *Silene*; Caryophyllaceae; Griechenland; taxonomy; EM; TW
- Gross, K. L. and J. D. Soule (1981). "Differences in biomass allocation to reproductive and vegetative structures of male and female plants of a dioecious, perennial herb, *Silene alba* (Miller) Krause." *American Journal of Botany* 68: 801-807.
Biomasse; *Silene*; Caryophyllaceae; reproduction; sex; dioecy; costs; TW
- Gunter, E. A. and Y. S. Ovodov (2002). "Changes in cell wall polysaccharides of *Silene vulgaris* callus during culture." *Phytochemistry* 59(7): 703-708.
Silene; cellbiology; Caryophyllaceae; callus; meristeme
In *Silene vulgaris* (M.) G. cell culture three growth phases were distinguished, namely, a lag phase, an exponential phase and a stationary phase. Pectin termed silenane and an acidic arabinogalactan were isolated as cell wall polysaccharides of *S. vulgaris* callus at the different growth phases during culture. Production of silenane as the galacturonan (or rhamnogalacturonan) core was observed at the beginning of the exponential phase and at the stationary phase of the callus growth. Arabinogalactan, containing the galacturonic acid residues, is formed at the exponential phase followed by attachment to the core of silenane in the middle of the exponential phase. The arabinogalactan constituent of silenane appeared to be destroyed gradually at the stationary growth phase. The monosaccharide compositions of silenane and arabinogalactan were determined at various phases of the callus growth. Silenane was found to be formed in maximum amounts at the exponential phase of the cell growth. Insignificant alterations of the yields of acidic arabinogalactan were found during culture while total productivity per litre of medium and rate of production per day of arabinogalactan were found to be maximal at the exponential phase of growth. (C) 2002 Elsevier Science Ltd. All rights reserved.
- Halket, A. C. (1931). "The flowers of *Silene saxifraga* L.; an inquiry into the cause of their day closure and the mechanism concerned in effecting their periodic movements." *Annals of Botany* 45: 15-37.
TW; *Silene*; flower; Caryophyllaceae; floral traits
- Hansen, T., H. R. Siegismund, et al. "Inbreeding depression and male reproductive allocation in *Silene nutans* (Caryophyllaceae)."
- Hauser, T. P. and V. Loeschcke (1994). "Inbreeding depression and mating-distance dependent offspring fitness in large and small populations of *Lychnis flos-cuculi* (Caryophyllaceae)." *Journal of Evolutionary Biology* 7: 609-622.
Inbreeding Depression; Mating Distance; Population Size; Caryophyllaceae; inbreeding depression; gene flow; fitness; TW; Europe; demography; breeding system
The spatial structure of four *Lychnis flos-cuculi* populations, varying in size and degree of isolation, was studied by comparing the fitness of offspring resulting from self-pollination and pollinations by neighbouring plants, plants within the same population, and plants from other populations. Selfed offspring had the lowest fitness of the four offspring groups. No significant difference was found between the performance of offspring from pollinations by neighbouring plants and offspring

pollinated by plants further apart but within the same population. A lower fitness of offspring from pollinations between neighbours would be expected if these matings, on average, yielded inbred offspring which suffered from inbreeding depression. These results imply that either a tight neighbourhood structuring is not present, or that the inbreeding depression for offspring by neighbours is too low to detect, although these are inbred. Crossings between populations produced offspring with a significantly higher fitness than offspring sired within populations. There were no significant differences in response to inbreeding among the populations, and differences in mean fitness among populations had no clear relation to the population size or degree of isolation. A reduce fitness of small populations due to inbreeding depression or a less severe response to experimental inbreeding due to purging of deleterious alleles is therefore not supported by our results.

- Hauser, T. P. and V. Loeschcke (1996). "Drought stress and inbreeding depression in *Lychnis flos-cuculi* (Caryophyllaceae)." *Evolution* 50: 1119-1126.
genetics; germination; phenology; reproduction; Caryophyllaceae; Wasserhaushalt; Wasserstreß; breeding system; inbreeding depression; TW
- Hauser, T. P. and H. R. Siegismund (2000). "Inbreeding and outbreeding effects on pollen fitness and zygote survival in *Silene nutans* (Caryophyllaceae)." *Journal of Evolutionary Biology* 13: 446-454.
U; TW; Caryophyllaceae; *Silene*; inbreeding; pollen; breeding system; autogamy; Ontogenie; reproduction; breeding system
- Hausmann, A. and S. Dötterl (2004). "Nectar plants and larval food-plants of the genus *Glossotrophia* (Geometridae, Sterrhinae): studies on pollne grains attached to museum specimens." *Nota lepidopterologica* 26(3/4): 127-136.
TW; Lepidoptera; Geometridae; pollen; nectar foraging; methods; herbivory; predation; interaction; Caryophyllaceae; *Silene*; *Dianthus*
- Hemborg, A. M. (1997). Reproductive allocation and costs of reproduction in subarctic herbs: a resource-based perspective. *Acta Universitatis Upsaliensis*. New York, Van Nostrand Reinhold: 35.
vegetation; TW; Schweden; Skandinavien; Europe; reproduction; resource allocation; Biomasse; Geschlechtsdimorphismus; Caryophyllaceae; *Silene*; Ranunculaceae; *Ranunculus*; *Trollius*; predation; seed
- Hemborg, A. M. (1998). "Seasonal dynamics in reproduction of first-year females and males in *Silene dioica*." *International Journal of Plant Sciences* 159(6): 958-967.
biomass allocation; Ustilaginales; nectar production; Caryophyllaceae; TW; *Silene*; reproduction; resource allocation; Biomasse; Geschlechtsdimorphismus; sex; dioecy; nectar
I examined the seasonal dynamics of reproduction for the first cohort of flowering males and females in *Silene dioica* in a greenhouse in subarctic Swedish Lapland. Reproductive investments in flowers, pollen or seeds, and nectar were compared between sexes in terms of biomass, nitrogen (N), phosphorus (P), and nectar volume. The onset of anthesis was concurrent, and male and female plants reached peak flower production at the same time. Throughout the season, female flowers produced on average 2.3 times more nectar than male flowers. However, because of the larger number of flowers per plant, males produced a total of six times more nectar than females. At peak flowering, male plants offered about 3.5 times more nectar than female plants. The chemical composition of pollen varied over the season. Pollen dry mass and N content per flower were at maximum levels during the most intense period of flowering. However, the P content of pollen per flower remained constant throughout the season. Flowers of male plants were collected at senescence, thus allowing for resorption of resources. Male flowers that naturally abscised during peak flowering contained more N and P than those that abscised at a later stage. However, the dry mass of male flowers did not vary over the season. A senescent fruit excluding seeds contained 7.5 (biomass), 4.4 (N), and 3.6 (P) times more than a male flower excluding pollen. In females, investments in seeds per flower were ca. 100 (biomass) or 45 (N and P) times higher compared with male investments in pollen. Male and female plants lost similar total amounts of biomass through senescent flowers during their first reproductive season. However, male plants invested and lost more nutrients through senescent flowers. Parallel with total estimates, the seasonal variation in reproductive allocation can give further insights to the roles of sexually dimorphic characters in dioecious plants.
- Hemborg, A. M. and P. S. Karlsson (1999). "Sexual differences in biomass and nutrient allocation of first-year *Silene dioica* plants." *Oecologia* 118(4): 453-460.

dioecy; reproductive effort; resource economy; nutrient allocation; Polymorphism; Caryophyllaceae; TW; *Silene*; dioecy; Geschlechtsdimorphismus; Biomasse; resource allocation; reproduction
 Reproductive and somatic biomass, nitrogen (N), and phosphorus (P) pools were compared between females and males in 1st-year plants of *Silene dioica*. We estimated irretrievable resources allocated to seeds, pollen, flowers, and unrecovered summer leaf investment by collecting plant parts at abscission throughout the season. At the end of the season, we determined resources lost through senescent stems and autumn leaf turnover and resources stored in perennial roots and overwintering buds. Sexual differences in allocation patterns depended on the resource used for comparison, and whether absolute or proportional resource pools were assessed. Total resource pools in terms of biomass and N were similar for females and males. However, male plants acquired relatively more P. The proportional reproductive investment, i.e., reproductive effort, was similar for males and females in terms of biomass and N. In terms of P, male reproductive effort was higher. There was no difference between sexes in the proportional and relative biomass allocated to perennial roots and overwintering buds. However, in terms of absolute and relative N allocation to belowground parts, females had larger reserves than males. Females, moreover, had a larger proportion of their P in below-ground parts. However, as male total P pools were larger, absolute P reserves did not differ between sexes. The high reproductive effort and N depletion of below-ground parts in males resulted largely from higher flower production compared to females. In females, seeds were the major component of reproductive effort. These results show that if biomass and nutrient allocation are assessed in parallel for dioecious plants, we obtain a more complete view of their sexual differences.

Hepper, F. N. (1951). "The variations of *Silene nutans* L. in Great Britain." *Watsonia* 2(2): 80-90.
 TW; *Silene*; Caryophyllaceae; Great Britain; Europe; morphology

Hermanutz, L. A. and D. J. Innes (1994). "Gender variation in *Silene acaulis* (Caryophyllaceae)." *Plant Systematics and Evolution* 191: 69-81.
 TW; Caryophyllaceae; sexual systems; Gynodioecy; Canada; breeding system; dioecy; sex; *Silene*; EM
Silene acaulis (Caryophyllaceae) is an alpine- arctic plant with a gynodioecious breeding system, but significant variation in sex expression has been reported. In addition, population sex ratio may be modified by the anther-smut *Microbotryum violaceum* (PERS.) DEML & OBERWINKLER, which sterilizes individuals of both sexes. A survey was undertaken at several sites on Baffin Island, Canada, to determine sex ratio and assess variation in female function among morphologically hermaphroditic individuals. The degree of anthersmut infection was also measured. Six sites had high female frequencies ranging from 72-80% and < 2% smut infection. High female frequencies may indicate cytoplasmic control of male-sterility. A seventh site from a mesic habitat had only 50% females and a higher rate of smut infection (22%). Of the three sites studied in detail, 84% of females set at least one capsule compared to only 25% of the hermaphrodites, indicating reduced female function. Hermaphrodites displayed significant variability in female function. Flowers with short styles (< 4.0 mm) had degenerated ovules, and field estimates confirmed that only 5% of these individuals set capsules, but comprised the majority (> 55%) of hermaphrodites. Although hermaphrodites with short-styled flowers functioned solely as males, there was no increase in pollen production compared to long-styled hermaphrodites. Long-styled hermaphrodites produced the same number of ovules as females, and all set at least one capsule but these plants were uncommon (< 11%) at all sites.

Herrera, C. M. (1996). Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. In: D. G. Lloyd and S. C. H. Barrett, *Floral Biology*. New York, Chapman & Hall: 65-87.
 TW; pollination; coevolution; entomophily; adaptation; floral traits; tubular flower; *Silene*; Caryophyllaceae; selection

Heslop-Harrison, J. and Y. Heslop-Harrison (1958). "Photoperiod, auxin and sex balance in a long-day plant." *Nature* 181: 100-102.
 TW; EM; Caryophyllaceae; *Silene*; sexual system; experiment; light; flowering phenology

Ingvarsson, P. K. and S. Lundberg (1993). "The effect of a vector-borne disease on the dynamics of natural plant populations: A model for *Ustilago violacea* infection of *Lychnis viscaria*." *Journal of Ecology* 81(2): 263-270.
 TW; Ustilaginales; parasitism; *Lychnis*; Caryophyllaceae; Modell; population; interaction
 1. A mathematical model was used to study how a parasitic castrating fungus affects the population dynamics of its host plant. The model is based on the interactions between the smut fungus *Ustilago*

violacea and its host plant *Lychnis viscaria*. The model also includes the pollination process as this plays a central role in the transmission of the fungal spores between plants. 2. Analysis of the model, with the disease absent, revealed that the pollinators have a limiting effect on the growth rate of the population. The model did not include any other density-dependent processes. 3. A condition was calculated which had to be satisfied to enable the disease to invade the host population and it is shown that the disease must possess a minimum transmission potential to be able to invade the host population. The condition was entirely dependent on the demographic processes of the host plant. The higher the recruitment rate of the host, the easier it is for the pathogen successfully to invade the host population. 4. When the disease was able to invade the host population, the disease incidence varied with the transmission potential of the fungal spores. If the disease incidence rose above c. 50%, the host population was driven to local extinction. This was mainly because, at high disease incidence levels, the fraction of pollinators that carried pollen was almost non-existent. This led to the transmission of the disease to all plants in the population and thus to the extinction of the entire host population.

- Janousek, B., S. Matsunaga, et al. (2002). "DNA methylation analysis of a male reproductive organ specific gene (MROS1) during pollen development." *Genome* 45(5): 930-938.
DNA; molecular biology; genetics; pollen; *Silene*;
Pollen grains of angiosperm plants represent a good model system for studies of chromatin structure and remodelling factors, but very little is known about the DNA methylation status of particular genes in pollen. In this study, we present an analysis of the DNA methylation patterns of the MROS1 gene, which is expressed in the late phases of pollen development in *Silene latifolia* (syn. *Meladrium album*). The genomic sequencing technique revealed similar DNA methylation patterns in leaves, binucleate pollen, and trinucleate pollen. Extremely high DNA methylation levels occurred in the CG dinucleotides of the upstream region (99%), whereas only a low level of CG methylation was observed in the transcribed sequence (7%). Low levels of methylation were also observed in asymmetric sequences (in both regions; 2% methylated). The results obtained in the MROS1 gene are discussed in consequence with the immunohistochemical data showing a hypermethylation of DNA in the vegetative nucleus.
- Jeanmonod, D. (1984). "Révision de la section Siphonomorpha Otth du genre *Silene* L. (Caryophyllaceae) en Méditerranée occidentale. III agrégat italica et espèces affines." *Candollea* 39: 549-639.
TW; *Silene*; monography; Caryophyllaceae; systematics; taxonomy; Europe; mediterranean
- Jeanmonod, D. (1984). "Révision de la section Siphonomorpha Otth du genre *Silene* L. (Caryophyllaceae) en Méditerranée occidentale. II le groupe du *S. mollissima*." *Candollea* 39: 195-259.
TW; *Silene*; monography; Caryophyllaceae; systematics; taxonomy; Europe; mediterranean;
- Jensen, K. (1998). "Species composition of soil seed bank and seed rain of abandoned wet meadows and their relation to aboveground vegetation." *Flora* 193(4): 345-359.
TW; seed bank; seed bank; succession; cluster analysis; grassland; litter; community; vegetation; meadow; regeneration; recruitment; Caryophyllaceae; *Lychnis*; *Silene*; statistics
Until the late fifties of this century species rich wet meadows were characteristic of the swampy alluvial plains in Schleswig-Holstein (north-western Germany). Today many of these meadows undergo successional changes due to abandonment. The vegetation development after abandonment can be characterised as a sequence of different successional stages. After an initial phase (successional stage I) follows a phase of clonal expansion of highly competitive species (successional stage II) and a phase of immigration and establishment (successional stages III and IV). In the course of succession species richness decreases and highly productive vegetation-stands develop. Species contributing to successional changes can either be present in the initial aboveground vegetation, in the soil seed bank or in the seed rain. The species composition of the seed bank and of the seed rain of different successional stages of abandoned wet meadows was investigated. Furthermore the relation between aboveground vegetation and seed bank and between aboveground vegetation and seed rain were determined using a cluster analysis. Seeds of some typical wet meadow (*Lychnis flos-cuculi*) and forage meadow species (*Cardamine pratensis*, *Cerastium holosteoides*, *Ranunculus repens*, *Poa trivialis*) are regularly present in the seed bank of later successional stages, whereas they are absent in the aboveground vegetation there. Thus the aboveground vegetation of permanent plots of the early successional stage I clusters with the seed bank of all permanent plots in the cluster analysis. On the other hand the aboveground vegetation of the permanent plots of the later successional stages II and III constitute cluster. The results of this study support the view, that even if the seed bank of later successional stages contains some species of earlier stages, the possibility to re-establish species rich meadows from species poor

fallows is relatively low. This is due to the fact, that seedling-densities of meadow species are decreasing exponentially during succession. Furthermore, rare or endangered plant species are scarcely ever found in the seed bank. The seed rain contains almost exclusively species of the aboveground vegetation present on the permanent plots and the surrounding area. No diaspores of characteristic meadow species were trapped in the seed traps, if these species were absent from the aboveground vegetation or did not produce seeds during the investigation period. Thus, the similarity of the aboveground vegetation of all permanent plots with the seed rain is very high; cluster analysis indicates that the aboveground vegetation of each permanent plot clusters with the seed rain of the same plot. The great similarity of the aboveground vegetation of all permanent plots with the seed rain is caused by the small dispersal distances of most of the occurring species. Both diaspores of herbaceous (*Urtica dioica*, *Galeopsis tetrahit* agg.) and woody (*Alnus glutinosa*, *Betula pubescens*, *Salix alba*) invasive species were trapped in seed traps in some cases. It can be concluded that the seed rain of abandoned wet meadows has an essential impact on progressive secondary succession (transition between successional stage II and III and between successional stage III and IV), while it has only a subordinate role in restoring species rich wet meadows from abandoned sites, that is in regressive succession.

- Jensen, K. and C. Meyer (2001). "Effects of light competition and litter on the performance of *Viola palustris* and on species composition and diversity of an abandoned fen meadow." *Plant Ecology* 155(2): 169-181.
TW; disturbance; recruitment; succession; meadow; community; vegetation; population; competition; litter; *Viola*; *Violaceae*; conservation biology; human disturbance
The effects of light competition and litter on seedling recruitment and the performance of established individuals were examined in *Viola palustris*. This polycarpic perennial plant was a common component of species-rich fen meadows in northwestern Germany until the middle of this century, but today is considered to be regionally endangered. From summer 1996 until summer 1998 a bi-factorial field experiment combining three standing crop treatments (mowing, thinning, control) with two litter layer treatments (litter removal, no litter removal) was carried out in an abandoned fen meadow to investigate the effects of these factors both on *V. palustris* and on aboveground species composition and diversity. MANOVAs (multivariate analysis of variance) revealed significant treatment effects for the performance of *V. palustris* related to experimental manipulation. Mowing increased vital attributes including the number of rosette leaves, the percentage of individuals with chasmogamous and cleistogamous flowers and the number of rhizomes. In contrast, the length of the leafstalk, mean leaf area and the length of rhizomes were negatively associated with mowing. Litter removal significantly increased the number of *V. palustris* seedlings. The removal of the litter layer already resulted in an increase in aboveground species richness in the first year of the experiment. After three years of experimental manipulation, both aboveground species richness and diversity were positively associated with mowing. Redundancy Analysis showed that typical wet meadow species (*Cardamine pratensis*, *Lychnis flos-cuculi*, *Lotus pedunculatus*) and species of mesotrophic fens (*Viola palustris*, *Agrostis canina*, *Potentilla palustris*) were positively influenced by mowing. It can be concluded that *V. palustris* recruitment and growth is promoted by a regular disturbance regime on fen meadows. The conservation of many typical species of wet meadows and fens in northwestern Germany depends on moderate grazing or cutting. These management types prevent successional changes which lead to an increase in standing crop and the development of a litter layer, both of which can cause local extinction.
- Jolls, C. L. and T. C. Chenier (1989). "Gynodioecy in *Silene vulgaris* (Caryophyllaceae): Progeny success, experimental design, and maternal effects." *American Journal of Botany* 76: 1360-1367.
Caryophyllaceae; sex; *Silene*; gynodioecy; experiment; germination; statistics; EM; TW
- Jolls, C. L., T. C. Chenier, et al. (1994). "Spectrophotometric analysis of nectar production in *Silene vulgaris* (Caryophyllaceae)." *American Journal of Botany* 81: 60-64.
methods; TW; anthesis; sugar; Geschlechtsdimorphismus; Caryophyllaceae; *Silene*; pollination; nectar
- Jones, V. and P. W. Richards (1962). "Biological flora of the British Isles." *Journal of Ecology* 50: 475-487.
TW; Great Britain; Europe; Flora; *Silene*; Caryophyllaceae; pollination; breeding system
- Juillet, N., H. Freymond, et al. (2003). "Isolation and characterization of highly polymorphic microsatellite loci in the bladder campion, *Silene vulgaris* (Caryophyllaceae)." *Molecular Ecology Notes* 3(3): 358-359.
bladder campion, microsatellite, *Silene vulgaris*

This study reports the isolation and characterization of seven highly polymorphic microsatellite loci in *Silene vulgaris* (Caryophyllaceae). The loci were isolated from two libraries constructed from genomic DNA enriched for CA and GA repeats. These markers yielded nine to 40 alleles per locus (mean 22.1) in a survey of 45 individuals from a single population located in the western Swiss Alps. Average observed heterozygosity ranged from 16.2 to 77.4%. These microsatellite loci should be valuable tools for studying fine-scale genetic structure.

- Jürgens, A., T. Witt, et al. (1996). "Reproduction and pollination in Central European populations of *Silene* and *Saponaria* species." *Botanica Acta* 109: 316-324.
Germany; TW; Europe; reproduction; Caryophyllaceae; *Silene*; pollination; entomophily; phalenophily; sphingophily; breeding system; EM; SB
- Jürgens, A., T. Witt, et al. (2002). "Pollen grain numbers, ovule numbers and pollen-ovule ratios in Caryophylloideae: Correlation with breeding system, pollination, life form, style number, and sexual system." *Sexual Plant Reproduction* 14(5): 279-289.
TW; Caryophyllaceae; *Silene*; *Dianthus*; P/O; breeding system; pollination; sex ratio; mating system; *Dianthus*; *Silene*; Caryophylloideae
Pollen-ovule ratios (P/O) were measured for 79 species of Caryophylloideae (*Agrostemma*, *Dianthus*, *Saponaria*, *Silene*, and *Vaccaria*). We analyzed if these features are best correlated with (1) the breeding system (outcrossing or selfing), (2) diurnal or nocturnal pollination, (3) life form (annual versus perennial), (4) style number, (5) the sexual system (hermaphroditism, gynodioecism, dioecism), or (6) the taxonomy of species. According to the classification of Cruden ((1977) *Evolution* 31:32-46) most species in the subfamily Caryophylloideae are facultative autogamous or facultative xenogamous. Autogamous or cleistogamous species showed significantly lower P/Os than xenogamy species. We found no differences between night- and day-flowering species; thus from our data diurnal and nocturnal flower visitors may be considered as equally efficient in transferring pollen. However, other factors are also important for the interpretation of P/Os. Pollen grain numbers and ovule numbers were found to correlate with style number, life form, and breeding system. The low P/Os of some dioecious, and therefore obligate outcrossing, species are discussed in relation to morphological traits that improve pollen deposition by pollinators on the stigma, and in relation to different flower numbers of male and female plants.
- Jürgens, A., T. Witt, et al. (2002). "Flower scent composition in night-flowering *Silene* species (Caryophyllaceae)." *Biochemical Systematics and Ecology* 30(5): 383-397.
TW; Caryophyllaceae; *Silene*; flower; scent; nocturnal; pollination; GC MS
Floral scent of 13 night-flowering *Silene* species (Caryophyllaceae) was collected by head-space adsorption and analysed via gas chromatography and mass spectrometry. Benzenoids together with isoprenoids dominated the scent in all species. Among the benzenoids, benzaldehyde (*Silene subconica* 35.5%, *Silene succulenta* 23.1%, *Silene sericea* 15.6%, *Silene vulgaris* 12.2%, and *Silene nutans* 9.9%), methylbenzoate (*Silene saxifraga* 96.1%, *S. succulenta* 15.2%), benzyl acetate (*Silene dichotoma* 37.8%, *S. nutans* 30.1%, *Silene italica* 9.0%, and *Silene latifolia* 5.5%), or benzyl alcohol (*Silene viscosa* 36.1%) occur in the largest amounts. p-Cresol is only found in the floral scent of *S. dichotoma* (28.5%). Among the isoprenoids, monoterpenes occur in the largest amounts (myrcene 23% in *Silene chlorantha*, trans-beta-ocimene 27.2% in *S. nutans* and 34.9% in *S. sericea*, fenchyl acetate 12.7% in *S. chlorantha*, beta-linalool 40.5% in *S. chlorantha* and 14.5% in *S. italica*). Relatively high amounts of lilac compounds occur in *S. latifolia* (49.1%), *Silene otites* (35.7%), *S. subconica* (15.2%), and *S. vulgaris* (59.6%). Higher amounts of sesquiterpenes (isoprenoids) were only found in *Silene vallesia* with beta-bourbonene and gamma-murolene. The vast majority of chemicals identified are common components of a wide array of scented angiosperm flowers. Nevertheless, the results conform most strongly with the findings in other night-blooming and/or moth-pollinated flowers. All investigated *Silene* species follow the general trend of floral scent compounds typical for moth-pollinated flowers, i.e. flowers having acyclic terpene alcohols (e.g. linalool), aromatic alcohols (benzyl alcohol, 2-phenylethanol) and esters derived from them, and small amounts of nitrogen-containing compounds. (C) 2002 Elsevier Science Ltd. All rights reserved.
- Jürgens, A., T. Witt, et al. (2003). "Flower scent composition in *Dianthus* and *Saponaria* species (Caryophyllaceae) and its relevance for pollination biology and taxonomy." *Biochemical Systematics and Ecology* 31(4): 345-357.
Caryophyllaceae; *Dianthus*; *Saponaria*; flower; scent; pollination; taxonomy; GC MS

Floral fragrance compounds of seven *Dianthus* species (*D. arenarius*, *D. armeria*, *D. barbatus*, *D. deltoides*, *D. monspessulanus*, *D. superbus*, and *D. sylvestris*) and one *Saponaria* species (*S. officinalis*) (Caryophyllaceae) were studied using headspace adsorption technique followed by gas chromatography massspectrometry (GC-MS). The number of compounds (fatty acid derivatives, benzenoids, phenyl propanoids, isoprenoids, and nitrogen containing compounds) identified in the floral odors ranged from 18 to 51 but all were dominated by only 1-3 compounds. Most of the compounds identified in this study have been previously reported in floral scents from species of the closely related genus *Silene* L. However, the phenyl propanoids eugenol, methyleugenol, methylisoeugenol, cis-asarone, and trans-asarone have formerly not been found in *Silene*. Based on the measurement of Sorensen's index of similarity (I-s) nonmetric multidimensional scaling (MDS) was used to detect meaningful underlying dimensions and to visualize similarities between the investigated species. The MDS analysis showed three groups of species, (1) the diurnal *D. armeria*, *D. barbatus*, and *D. deltoides* are characterized by the predominance of fatty acid derivatives, (2) the closely related nocturnal *D. monspessulanus*, and *D. superbus* by high relative amounts of isoprenoids such as cis-beta-ocimene and beta-caryophyllene, and (3) the species *D. arenarius*, *D. sylvestris* and *S. officinalis* by a predominance of benzenoids, especially methylbenzoate. The results are discussed in relation to pollination, especially by butterflies, moths, and hawkmoths. (C) 2002 Elsevier Science Ltd. All rights reserved.

- Kaltz, O. and J. A. Shykoff (2001). "Male and female *Silene latifolia* plants differ in per-contact risk of infection by a sexually transmitted disease." *Journal of Ecology* 89: 99-109.
TW; *Silene*; dioecy; dimorphism; parasitism; Ustilaginales; Caryophyllaceae; pathogen; infection; Mycophyta
- Kay, Q. O. N. (1981). Intraspecific discrimination by pollinators and its role in evolution. In: J. A. Armstrong, J. M. Powell and A. J. Richards, *Pollination and Evolution*. Sydney, Royal Botanical Gardens: 9-28.
pollination; evolution; coevolution; pollinator behavior; TW; sex; Geschlechtsdimorphismus; floral traits; interaction; *Silene*; dioecy; Asteraceae; Caryophyllaceae; Dipsacaceae; Brassicaceae; color
- Kay, Q. O. N., A. J. Lack, et al. (1984). "Differences between sexes in floral morphology, nectar production and insect visits in a dioecious species *Silene dioica*." *New Phytologist* 98(3): 515-530.
EM; TW; Caryophyllaceae; *Silene*; sexual system; morphology; nectar; pollinator behavior; Geschlechtsdimorphismus
S. dioica (L.) Clairv. was studied in several wild populations near Swansea [UK] and in an experimental population to determine the extent of differences between the sexes in floral morphology, nectar production, and insect visits to flowers, and the effects of these differences on seed set. Male flowers are larger than female flowers and are borne more densely over a longer period. Male flowers have longer and more frequently white corona scales which may mimic the projecting white styles of female flowers. Male and female flowers were observed to secrete similar quantities of nectar sugar on the 1st morning of opening, but female flowers secreted more than males subsequently, and the total volumes of nectar secreted by female flowers were considerably greater. Male plants varied more than females in the total quantity of nectar sugar secreted per flower. Nectar concentration was nearly always greater in male flowers than in female flowers. Bumblebees, particularly *Bombus hortorum* (L.), *B. pascuorum* (Scop.) and *B. terrestris* (L.), were the most important visitors to the flowers of *S. dioica* in the study sites, with some honeybees [*Apis mellifera* (L.)], butterflies (mainly Pieridae) and hoverflies (Syrphidae). Some visitors, including those that were most numerous at some sites, made most or all of their visits illegitimately. In the field in 1980 many visitors discriminated in favor of male flowers, which were much more numerous than female flowers. In the experimental population in 1981, many visitors discriminated in favor of female flowers, which were more numerous than in the field populations but were still substantially outnumbered by male flowers. Some individual bumblebees showed a change in preferences during the day, discriminating in favor of female flowers only during the afternoon, when the nectar resources available from female flowers were proportionately greater. The total numbers of visits that were observed to female and male flowers in the experimental population corresponded closely with the total quantities of nectar sugar available from each sex. The importance of the different insect visitors and of their discrimination between sexes in pollination is discussed. Seed set apparently was not reduced by discrimination or insufficiency of pollinator visits in closely spaced plants, but was reduced in plants isolated by distances of 15 m or greater.
- Kephart, S. R., E. Brown, et al. (1999). "Inbreeding depression and partial selfing: Evolutionary implications of mixed-mating in a coastal endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae)." *Heredity* 82: 543-554.

TW; *Silene*; Caryophyllaceae; reproduction; seed set; demography; autogamy; inbreeding depression; Autogamy; breeding system

Recent studies have found moderate to high levels of selfing in plants despite high inbreeding depression. Because both factors influence the evolution and persistence of rare plants, we conducted glasshouse and field studies of pollination and inbreeding in *Silene douglasii* var. *oraria*, a perennial tetraploid endemic to coastal prairies. We detected: (i) variation in reproduction or inbreeding depression among life stages, years and maternal families; (ii) partial selfing yet higher relative fitness in outcrossed than selfed progeny; (iii) differing values of selfing and inbreeding depression using population means vs. matched maternal families. Fruit and seed production varied significantly with pollination treatment and year in flowers manipulated in situ during three seasons of growth. Hand-pollinations providing pollen in excess of ovule production in 1996 yielded more seeds than marked, open-pollinated flowers, implying pollen limitation of seed production. However, among-year differences in reproductive success after open-pollination (i.e. values equivalent to autogamy, selfing or xenogamy) suggest that pollination levels also vary temporally. In pollinations matched by maternal family, selfing yielded significantly fewer seeds than outcrossing. Fitness differences between inbred and outbred progeny were significant ($P < 0.05$) for seed production, percentage germination, and biomass or fecundity, but not for survival. Maternal family data gave selfing rates intermediate between obligate outcrossers and predominant selfers ($S = 0.34-0.51$), but population-wide means gave unusually high values ($S = 1.1-1.6$). Cumulative inbreeding depression was 76% for maternal families, and 70-85% using population means; in all cases, inbreeding depression values were high in early and late life stages, and lowest for survival. Thus far, reproductive assurance offers the most cogent explanation for the coexistence of moderate selfing and high inbreeding depression in this strongly protandrous *Silene* once thought to be highly xenogamy. This possibility merits further study in other rare plants with mixed-mating systems, where inbreeding depression and pollinator scarcity may both compromise population persistence and raise the threshold below which selfing is favoured by evolution.

Kephart, S. R., K. Sturgeon, et al. (1999). "Varietal relationship in *Silene douglasii* (Caryophyllaceae): Morphological variability at the population level." *Systematic Botany* 24(4): 529-544.

TW; *Silene*; Caryophyllaceae; population; demography; morphology; evolution; variability

Kiefer, K. N., K. R. Okey, et al. "Ecological genetics of white campion (*Silene latifolia*) seed banks - a comparison of light and dark germination among maternal families." Internet.

TW; *Silene*; Caryophyllaceae; germination; Samenbank; demography

Klapp and Opitz von Doberfeld Caryophyllaceae - Kräuterbestimmungsschlüssel. In, P. Pary: 104-111.

TW; Caryophyllaceae; key; *Silene*

Knuth, P. (1898). Caryophyllaceae. In, *Handbuch der Blütenbiologie*. Leipzig, Verlag Wilhelm Engelmann: 154-177.

pollination; Caryophyllaceae; *Silene*; flower; morphology; TW

Kruckeberg, A. R. (1955). "Interspecific hybridizations of *Silene*." *American Journal of Botany* 42: 373-378.

hybrid; breeding system; *Silene*; Caryophyllaceae; TW

Kruckeberg, A. R. (1960). "Chromosome numbers in *Silene* (Caryophyllaceae). II." *Madroño* 15: 205-215.

genetics; Polyploidie; *Silene*; Caryophyllaceae; Karyosystematik; TW

Ladero, T., S. RivasMartinez, et al. (1999). "New hybrid of genus *Silene* (Caryophyllaceae) in the Serra da Estrela, Portugal." *Botanical Journal of the Linnean Society* 130(1): 69-80.

Iberian Peninsula; seed; Caryophyllaceae; TW; *Silene*; systematics; taxonomy; hybrid; Portugal; Iberische Halbinsel; Europe; mediterranean; seed; morphology; SEM; ecology

A description is given of a new hybrid of the genus *Silene* (Caryophyllaceae) found in the Serra da Estrela Portugal. A brief taxonomic review of the two parent species, whose correct denomination has been controversial since the last century, is followed by a botanical description of the new taxon, *Silene* x *montistellensis* nothosp. Nov. SEM study of its seeds revealed the presence of clear morphological characters which are useful for simple identification and differentiation. A section on the ecology and phytosociology of the three taxa includes the different affinities of each element for substrate type and plant community in which their optimum is reached. Finally, we list all the herbarium specimens from Portuguese sites consulted, both from our own collections and from different Spanish and Portuguese herbaria. Using the data from these Portuguese specimens and

from field notes two comparative tables of morphological characters are presented. (C) 1999 The Linnean Society of London.

- Laghettie, G. (1994). "Notes on economic plants. Utilization of *Silene vulgaris* (Moench) Garcke in Italy." *Economic Botany* 48: 337-339.
Silene; TW; Caryophyllaceae; Nutzpflanzen; Italien; Europe
- Lammi, A., P. Siikamäki, et al. (1999). "Genetic diversity, population size, and fitness in central and peripheral populations of a rare plant *Lychnis viscaria*." *Conservation Biology* 13(5): 1069-1078.
TW; genetic diversity; molecular biology; population; size; fitness; *Lychnis*; *Silene*; Caryophyllaceae; Genetic diversity is expected to decrease in small and isolated populations as a consequence of bottlenecks founder effects, inbreeding, and genetic drift. The genetics and ecology of the rare perennial plant *Lychnis viscaria* (Caryophyllaceae) were studied in both peripheral and central populations within its distribution area. We aimed to investigate the overall level of genetic diversity its spatial distribution, and possible differences between peripheral and central populations by examining several populations with electrophoresis. Our results showed that the level of genetic diversity varied substantially among populations ($H_{exp} = 0.000-0.116$) and that the total level of genetic diversity (mean $H_{exp} = 0.056$) was low compared to that of other species with similar life-history attributes. The peripheral populations of *viscaria* had less genetic variation (mean $H_{exp} = 0.034$) than the central ones (0.114). Analysis of genetic structure suggested limited gene flow (mean $F_{ST} = 0.430$) and high differentiation among populations emphasizing the role of genetic drift ($N(e)m = 0.33$). Isolation was even higher than expected based on the physical distance among populations. We also focused on the association between population size and genetic diversity and possible effects on fitness of these factors. Population size was positively correlated with genetic diversity. Population size and genetic diversity, however, were not associated with fitness components such as germination rate, seedling mass or seed yield. There were no differences in the measured fitness components between peripheral and central populations. Even though small and peripheral populations had lower levels of genetic variation, they were as viable as larger populations, which emphasizes their potential value for conservation.
- Laporte, M. M. and L. F. Delph (1996). "Sex-specific physiology and source-sink relations in the dioecious plant *Silene latifolia*." *Oecologia* 106(1): 63-72.
sex; dioecy; *Silene*; Caryophyllaceae; physiology; reproduction; costs; costs; resource allocation; Geschlechtsdimorphismus
Differences in reproductive demands between the sexes of dioecious plants could cause divergence in physiology between the sexes. We found that the reproductive effort of female *Silene latifolia* plants increased to more than twice that of male plants or female plants that were prevented from setting fruit by lack of pollination after 4 weeks of flowering. Whole-plant source/sink ratios of pollinated females were significantly lower than those of males or unpollinated females because of investment in fruit. We hypothesized that these differences in source/sink ratio between the sexes and within females, depending on pollination, would lead to differences in leaf photosynthetic rates. Within females, we found that photosynthetic capacity was consistent with measurement of whole-plant source/sink ratio. Females that were setting fruit had 30% higher light-saturated photosynthetic rates by 28 days after flowering than females that were not setting fruit. Males, however, had consistently higher photosynthetic rates than females from 10 days after flowering onwards. Males also had approximately twice the dark respiration rates of fruiting females. We found that female reproductive structures are longer-lived and contribute more carbon to their own support than male reproductive structures. Despite the higher rates of leaf dark respiration and lower calyx photosynthetic rates, males fix more carbon than do females. We conclude that females have a sink-regulated mechanism of photosynthesis that allows them to respond to variations in fruit set. This mechanism is not, however, sufficient to explain why male *S. latifolia* plants have higher rates of photosynthesis, higher source/sink ratios, and lower reproductive allocation, but fail to grow larger than female plants.
- Lardon, A., S. Georgiev, et al. (1999). "Sexual dimorphism in white campion. Complex control of carpel number is revealed by Y chromosome deletions." *Genetics* 151(3): 1173-1185.
Caryophyllaceae; TW; *Silene*; dioecy; Geschlechtsdimorphismus; genetics; DNA; Chromosom
Sexual dimorphism in the dioecious plant white campion (*Silene latifolia* = *Melandrium album*) is under the control of two main regions on the Y chromosome. One such region, encoding die gynoeceum-suppressing function (GSF), is responsible for the arrest of carpel initiation in male flowers. To generate chromosomal deletions, we used pollen irradiation in male plants to produce

hermaphroditic mutants (*bsx* mutants) in which carpel development was restored. The mutants resulted from alterations in at least two GSF chromosomal regions, one autosomal and one located on the distal half of the (p)-arm of the Y chromosome. The two mutations affected carpel development independently, each mutation showing incomplete penetrance and variegation, albeit at significantly different levels. During successive meiotic generations, a progressive increase in penetrance and a reduction in variegation levels were observed and quantified at the level of the Y-linked GSF (GSF;Y). Possible mechanisms are proposed to explain the behavior of the Dss mutations: epigenetic regulation or/and second-site mutation of modifier genes. In addition, studies on the inheritance of the hermaphroditic trait showed that, unlike wild-type Y chromosomes, deleted Y chromosomes can be transmitted through both the male and the female lines. Altogether, these findings bring experimental support, on the one hand, to the existence on the Y chromosome of a genic meiotic drive function(s) and, on the other hand, to models that consider that dioecy evolved through multiple mutation events. As such, the GSF is actually a system containing more than one locus and whose primary component is located on the Y chromosome.

- Lassere, T. B., S. B. Carroll, et al. (1996). "Effect of pollen competition on offspring quality at ranging stages of the life cycle in *Silene latifolia* Poiret (L.)." *Bulletin of the Torrey Botanical Club* 123: 175-179.
pollen; competition; *Silene*; Caryophyllaceae; pollination; reproduction; EM; TW; fitness
- Law, T. F., S. Lebel-Hardenack, et al. (2002). "Silver enhances stamen development in female white campion (*Silene latifolia* [Caryophyllaceae])." *American Journal of Botany* 89(6): 1014-1020.
TW; Caryophyllaceae; *Silene*; metal; stamen; development; sex; dimorphism; flower; ontogeny
Sex expression in the dioecious plant white campion (*Silene latifolia* Poiret subsp. *alba*) appears to be insensitive to exogenous applications of auxins, cytokinins, gibberellic acid, and ethylene however, silver thiosulfate (Ag₂S₂O₃) an ethylene inhibitor enhanced stamen development in female white campion. In wild-type females. stamen development is arrested before the microspore mother cells are formed. In contrast. stamens of Ag₂S₂O₃-treated females completed meiosis and produced microspores. Stamen development for these females was incomplete. however. and pollen did not mature. Ag₂S₂O₃ stimulated stamen development to the same extent in asexual white campion mutants that retained a Y chromosome but had lost Y-linked gene, needed for early stages of stamen development Although Ag₂S₂O₃ can inhibit ethylene signaling, the enhancement of stamen development in female white campion cannot be explained as a loss of ethylene response because no other ethylene inhibitor tested (1-methylcyclopropene, trans-cyclooctene, aminoethoxyvinylglycine, and cobalt chloride) caused stamens to develop in female plants, In addition, application of other metal ions could not enhance stamen development. Therefore, the effect we observed on female white campion was specifically caused by silver ions but not by their action on ethylene signaling.
- Lee, J. A. (1981). "Variation in the infection of *Silene dioica* (L.) Clairv. by *Ustilago violacea* (Pers.) Fuckel in North West England." *New Phytologist* 87: 81-89.
Silene; Caryophyllaceae; Great Britain; Europe; Ustilaginales; Mycophyta; TW; parasitism; INFECTION; interaction
- Lesica, P. (1999). "Effects of fire on the demography of the endangered, geophytic herb *Silene spaldingii* (Caryophyllaceae)." *American Journal of Botany* 86(7): 996-1002.
TW; Caryophyllaceae; demography; fire; population; dormancy; *Silene*; community; germination; vegetation; succession
Understanding the effects of disturbances such as fire on plant demography helps elucidate the mechanisms that cause changes in community composition. I studied the effects of spring and fall fires on *Silene spaldingii*, an endangered perennial herb of grasslands in northwest Montana. Individual *S. spaldingii* plants were mapped, and size and flowering were recorded for 1 yr prior and 5 yr subsequent to the burn treatments. Enhanced seedling recruitment (70-410%) and a 22% increase in population size were the principal effects of fire on *S. Spaldingii*, and fall burn plots had lower recruitment than spring burn plots. These effects were apparent for 2-3 yr following the treatments. Fire had no detectable effect on the survival of adults or recruits of *S. Spaldingii*. *Silene spaldingii* exhibits prolonged dormancy in which plants do not produce aboveground vegetation for one to several consecutive years. Results suggest that fire has a positive effect on the population dynamics of *S. spaldingii* by removing litter and creating safe sites for recruitment. Prescribed fire should be an important tool for managing populations of this rare plant.
- Liden, M., M. Popp, et al. (2001). "A revised generic classification of the tribe *Sileneae* (Caryophyllaceae)." *Nordic Journal of Botany* 20(5): 513-518.

TW; systematics; Caryophyllaceae; *Silene*; molecular biology; taxonomy; monography; phylogeny
A reclassification of the tribe *Sileneae* compatible with molecular data is presented. The genus *Eudianthe* (*E. laeta* and *E. coeli-rosa*) is restored. *Viscaria*, *Heliosperma*, and *Atocion* together form a well supported monophyletic group distinct from *Silene* and *Lychnis*, and are recognized at generic level. With *Agrostemma* and *Petrocoptis*, the number of genera in the tribe sums up to eight. The new combinations *Silene samojedorum*, *Silene ajanensis*, *Lychnis abyssinica*, *Atocion asterias*, *Atocion compactum*, *Atocion lerchenfeldiana*, and *Atocion rupestre* are made.

- Longo, C. P. (1994). Genes controlling sex expression. In: E. G. Williams and e. al., Genetic control of self-incompatibility and reproductive development in flowering plants. Netherlands, Kluwer Academic Publishers: 245-265.
Silene; TW; sex; genetics; breeding system; sex ratio
- Lorenz, H. (1998). Untersuchungen zur geschlechtsspezifischen Unterschieden der Mortalitätsrate der Ohrlöffel-Lichtnelke *Silene otites* (L.) Wibel (Caryophyllaceae) unter verschiedenen Bedingungen und zu Ausbreitungsmechanismen des Brandpilzes *Microbotryum major* (J. Schröter) G. Deml & F. Oberwinkler (Ustilaginales) in populationen von *Silene otites*. Institut für Geobotanik und Botanischer Garten. Halle, Martin-Luther-Universität Halle-Wittenberg: 81.
TW; *Silene*; Caryophyllaceae; Ustilaginales; anther smut disease; sex; dimorphism; fitness; reproduction; life form; germany; Europe
- Lovett Doust, J., G. O'Brien, et al. (1987). "Effect of density on secondary sex characteristics and sex ratio in *Silene alba* (Caryophyllaceae)." *American Journal of Botany* 74: 40-46.
sex; *Silene*; Caryophyllaceae; demography; reproduction; sexual system; TW; sex ratio; population
- Lundqvist, A. (1995). "Concealed genes for self-incompatibility in the carnation family Caryophyllaceae?" *Hereditas* 122: 85-89.
EM; TW; self incompatibility; Caryophyllaceae; *Cerastium*; genetics; polymorphism; autogamy; *Dianthus*; *Lychnis*; *Silene*; reproduction; seed set
- Lyons, E. E., D. Miller, et al. (1994). "Evolutionary dynamics of sex ratio and gender dimorphism in *Silene latifolia*. 1. Environmental effects." *Journal of Heredity* 85: 196-203.
dioecy; AJ; *Silene*; sex; Caryophyllaceae; evolution; breeding system; pollination; TW; Geschlechtsdimorphismus; sex ratio
In 10 sibships of the dioecious *Silene latifolia*, we studied effects of maternal family on sex ratio and effects of maternal family, plant density, and watering regime on sexual dimorphism. Plant sex ratio was female biased; the significant heterogeneity across families was consistent with a hypothesis of genetic variation for progeny sex ratio, expressed before seed germination. Floral sex ratios were male biased and heterogenous across families; males had many more flowers than females. All traits (biomass, flower number, height, longest branch length, branch number, and flower weight) showed sexual dimorphism. We documented genetic variation in the degree of sexual dimorphism in plant height and in the dimorphic response of flower weight to watering regime. Family mean genetic correlations between females and males were significantly positive for all traits except flower weight. These correlations varied significantly across growing environments for plant height and branch number, suggesting that only in certain environments will such positive correlations act to genetically constrain further dimorphism. The pattern of genetic correlation among traits was very similar in females and males and was not environmentally variable. Under the best growing conditions, however, females exhibited stronger correlations among traits and so were genetically more constrained than males. Female plants grown under water stress showed many negative genetic correlations, a response typical of resource limitation.
- Lyons, E. E., D. Miller, et al. (1994). "Evolutionary dynamics of sex-ratio and gender dimorphism in *Silene latifolia* .1. Environmental effects." *Journal of Heredity* 85(3): 196-203.
life history; genetics; dioecy; sex; phenotype; biomass; Caryophyllaceae; sex ratio; density; demography; variation; dimorphism; resource allocation
In 10 sibships of the dioecious *Silene latifolia*, we studied effects of maternal family on sex ratio and effects of maternal family, plant density, and watering regime on sexual dimorphism. Plant sex ratio was female biased; the significant heterogeneity across families was consistent with a hypothesis of genetic variation for progeny sex ratio, expressed before seed germination. Floral sex ratios were male biased and heterogenous across families; males had many more flowers than females. All traits (biomass, flower number, height, longest branch length, branch number, and flower weight) showed sexual dimorphism. We documented genetic variation in the degree of sexual dimorphism in

plant height and in the dimorphic response of flower weight to watering regime. Family mean genetic correlations between females and males were significantly positive for all traits except flower weight. These correlations varied significantly across growing environments for plant height and branch number, suggesting that only in certain environments will such positive correlations act to genetically constrain further dimorphism. The pattern of genetic correlation among traits was very similar in females and males and was not environmentally variable. Under the best growing conditions, however, females exhibited stronger correlations among traits and so were genetically more constrained than males. Female plants grown under water stress showed many negative genetic correlations, a response typical of resource limitation.

Lyons, E. E., N. Shah-Mahoney, et al. (1995). "Evolutionary dynamics of sex ratio and gender dimorphism in *Silene latifolia* L. Sex ratio and flowering status in a potentially male-biased population." *Journal of Heredity* 86: 107-113.

dioecy; Caryophyllaceae; *Silene*; Geschlechtsdimorphismus; sex; pollination; seed; germination; SB; TW; sex ratio

Macior, L. W. (1978). "The pollination ecology and endemic adaptation of *Pedicularis furbishiae*." *Bulletin of the Torrey Botanical Club* 104(5): 268-277.

pollination; Scrophulariaceae; melittophily; endemism; *Bombus*; pollinator behavior; community A study of the rare, endemic *P. furbishiae* in the St. John River Valley of northern Maine [USA] indicated a preference of the plant for calcareous, well-drained sandy loam of transient river terrace habitats in close, consistent association with *Alnus crispa* but no root parasitism with any host plants. It was self-incompatible and obligately pollinated by workers of *Bombus vagans* which were coadapted to the pollination mechanism morphologically and behaviorally. *P. furbishiae* was observed to reproduce by seed only and in sufficient numbers to maintain and possibly increase the size of the presently known total population of .apprx. 600 plants. Pollination interrelationships with *Epilobium angustifolium*, *Trifolium pratense*, *Vicia cracca* and other *Bombus* spp. [*B. fervidus*, *B. ternarius* and *B. terricola*] pollinated members of the *Pedicularis* plant community [*Rosa acicularis*, *Silene cucubalus*, *Spiraea latifolia*, *Thalictrum dasycarpum* and *Trifolium hybridum*] were also examined. Bumblebees were only 25% constant in their foraging for pollen. Techniques employed included chemical and physical soil analyses, atmospheric measurements, insect enclosure and artificial pollination, nectar analysis by refractometry, reflectance spectrophotometry of corolla color, microscopic analysis of corbicular pollen loads, measurement of corresponding insect and floral dimensions, cinematographic analysis and recording of pollinator behavior, and quadrat analysis of *Pedicularis* distribution.

Malm, J. U. and H. C. Prentice (2002). "Immigration history and gene dispersal: allozyme variation in Nordic populations of the red campion, *Silene dioica* (Caryophyllaceae)." *Biological Journal of the Linnean Society* 77(1): 23-34.

TW; gene flow; geography; variation; glacial refugia; pollen; dispersal; seed; migration; allozyme; Europe; genetics; biodiversity; population; demography

Most of the Nordic region was ice-covered during the last (Weichselian) glaciation. During the postglacial period, plant and animal species recolonized the region from several directions and the geographic structuring of genetic variation within Nordic species may still contain a historic component that reflects patterns of postglacial immigration. The present investigation of 69 populations of *Silene dioica* represents the first large-scale allozyme study of a widespread herbaceous plant in the Nordic region. Although the frequencies of individual alleles showed a range of different geographic patterns, mapping of the axis scores from an ordination of variation at eight polymorphic loci revealed a division into two main geographic groups of populations. The broadly south-western and northeastern distributions of these two groups of populations suggest that immigration into the region may have involved both eastern and southern geographic sources. However, the geographic boundaries between the two groups of populations are diffuse, and the relatively low between-population component of genetic diversity ($G(ST) = 16.4\%$) suggests a history of extensive gene dispersal by pollen. (C) 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 23-34.

Mamadalieva, N. Z., L. N. Zibareva, et al. (2003). "Phytoecdysteroids of *Silene viridiflora*." *Chemistry of Natural Compounds* 39(2): 199-203.

Silene; Caryophyllaceae; steroid hormones; compounds

The known ecdysteroids polipodin B, 2-deoxyecdysterone, ecdysterone, 26-hydroxypolipodin B, integristerone A, and sileneosides A and D were observed in the aerial part of *Silene viridiflora* L. (Caryophyllaceae). 26-Hydroxypolipodin B was observed in this species for the first time.

- Marsden-Jones, E. M. and W. D. Turrill The bladder campions. London, Ray Society.
TW; textbook; *Silene*; Caryophyllaceae; systematics; taxonomy; pollination; reproduction; morphology
- Mastenbroek, O., H. C. Prentice, et al. (1983). Patterns of variation in European *Silene pratensis* - morphological and biochemical character sets. 7th Symposium Morphology, Anatomy, and Systematics, Amsterdam, Koninklijke Nederlandse Botanische Vereniging; Deutsche Botanische Gesellschaft.
Silene; Caryophyllaceae; Europe; demography; compounds; pollen; morphology; seed; systematics; taxonomy; TW
- Mastenbroek, O., H. C. Prentice, et al. (1983). Patterns of variation in European *Silene pratensis* - pollen morphology. 7th Symposium Morphology, Anatomy, and Systematics, Amsterdam, Koninklijke Nederlandse Botanische Vereniging; Deutsche Botanische Gesellschaft.
Silene; Caryophyllaceae; Europe; demography; compounds; pollen; morphology; seed; systematics; taxonomy; TW
- Maurice, S. (1999). "Gynomonoecy in *Silene italica* (Caryophyllaceae) - Sexual phenotypes in natural populations." *Plant Biology* 1(3): 346-350.
TW; sex ratio; flowering phenology; gynodioecy; gynomonoecy; *Silene*; Caryophyllaceae; polymorphism; sex; breeding system; phenology
Some gynodioecious species present not only hermaphrodite and female individuals but also gynomonoecious individuals that produce both female and perfect flowers. In a study of natural populations of *Silene italica*, we found that gynomonoecious individuals were common in all populations (from 13 to 39%) and that their frequency was independent of the frequency of females. No relationship was found between the number of flowers a plant produced and its sex. The majority of gynomonoecious individuals showed a low proportion of female flowers but all proportions were found. Female flowers of these individuals were well-developed flowers that set fruit as often as female flowers on pure females. The percentage fruit set was characteristic of the type of flowers (around 56% for perfect flowers and 76% for female flowers) whatever the sex of the individual plant. The determination of sex is not known but data indicate that environmental conditions could be responsible for a shift between the hermaphrodite and the gynomonoecious states rather than between the female and the gynomonoecious states.
- Maurice, S., C. Desfeux, et al. (1998). "Is *Silene acaulis* (Caryophyllaceae) a trioecious species? Reproductive biology of two subspecies." *Canadian Journal of Botany* 76(3): 478-485.
TW; trioecy; subdioecy; dioecy; Caryophyllaceae; *Silene*; breeding system; sex; trioecy; androdioecy; morphology; floral traits; fruit set; population
Based on morphological characters, *Silene acaulis* subsp. *exscapa* and *Silene acaulis* subsp. *cenisia* have been previously described as dioecious and trioecious, respectively. Here we examine whether these subspecies are truly dioecious (subsp. *Exscapa*) and trioecious (subsp. *cenisia*) based on individual seed and pollen production. Nine populations of subsp. *cenisia* and five populations of subsp. *Exscapa* were studied in the French Alps. The ratio of staminate to female plants within populations did not in general differ from 1:1, the sex ratio expected in dioecious populations. Staminate plants of both subspecies were found to set fruits. In subsp. *Exscapa*, the ratio of fruit production in female versus staminate plants is around 900; in subsp. *Cenisia*, this ratio is around 10. The advantage of female plants in fruit production is not always sufficient to explain their frequencies in natural populations. Staminate plants cannot be divided in two distinct categories: males and hermaphrodites. The two subspecies can be best described as subdioecious, although *S. subsp. exscapa* is effectively closer to exhibiting true dioecy than *S. subsp. cenisia*.
- Mayer, E. and G. Gottsberger (2000). "Pollen viability in the genus *Silene* (Caryophyllaceae) and its evaluation by means of different test procedures." *Flora* 195: 349-353.
TW; *Silene*; pollen viability; trinucleate pollen; in vitro ; aniline blue in lactophenol staining; fluorochromatic; reaction; Caryophyllaceae; pollen; methods; pollen germination; pollen Tube
Various direct and indirect tests are used to estimate pollen viability. Results obtained with these tests, however, are contradictory for different species and do not always match with naturally occurring pollen germination. To investigate naturally occurring pollen germination of four *Silene* species a new method of scoring germinated pollen grains in vivo directly on the stigmas of intact flowers was developed. Germination percentages found with the in vivo test ranged from 67 to 77%. The results of two indirect tests that are commonly used to assess pollen viability, aniline blue in

lactophenol staining (ALS) and fluorochromatic reaction (FCR), were compared with the results of the newly developed in vivo test for the same four species. ALS revealed high pollen viability, ranging from 82 to 93%, whereas FCR revealed lower viability, ranging from 28 to 50%. Our suspicion that ALS overestimates natural pollen germination in *Silene* was confirmed by testing viability of dry-stored and n-Hexane-stored pollen grains with both indirect tests. Because of the known short viability of trinucleate pollen grains, dry-stored grains should be dead. Storage in n-Hexane, however, conserves pollen viability because of its positive effect on the integrity of the pollen membrane. ALS showed high viability for both dry-stored and n-Hexane-stored pollen grains. In contrast, FCR-treated pollen showed viability only after n-Hexane-storing but not after dry-storing. Of the two indirect tests, FCR should be given preference over ALS because it reflects at least trends of viability in pollen grains, however, it is not accurate enough to reflect natural germination percentages of trinucleate *Silene* pollen as found with the in vivo test.

McCauley, D. E. (1997). "The relative contribution of seed and pollen movement to the local genetic structure of *Silene alba*." *Journal of Heredity* 88: 257-263.

TW; dispersal; gene flow; *Silene*; Caryophyllaceae; population; demography; long distance dispersal; genetics

McCauley, D. E. (1998). "The genetic structure of a gynodioecious plant: Nuclear and cytoplasmic genes." *Evolution* 52(1): 255-260.

cpDNA; gene flow; gynodioecy; population;

Sex expression in gynodioecious plants is often determined by an interaction between biparentally and maternally inherited genes. Their relative rates of gene flow should be considered when modeling the evolution of the sex ratio in structured populations. In order to understand patterns of gene flow in *Silene vulgaris*, a gynodioecious plant, genetic structure was estimated from biparentally inherited genetic markers (allozymes) and a maternally inherited marker (chloroplast DNA) using Wright's F-st. Based on data from 16 local populations, chloroplast DNA showed considerably more genetic structure than did allozymes (F-st values of 0.62 and 0.22, respectively). This suggests that the rate of gene flow is about three times greater for nuclear genes.

McCauley, D. E. and M. T. Brock (1998). "Frequency-dependent fitness in *Silene vulgaris*, a gynodioecious plant." *Evolution* 52(1): 30-36.

frequency; selection; gynodioecy; population; sex ratio; *Silene*; Caryophyllaceae; fitness; gene flow; breeding system;

In gynodioecious plants the selective processes that determine the relative number of female and hermaphroditic individuals are often frequency dependent. Frequency-dependent fitness can occur in the two sexes through a variety of mechanisms, especially given pollen limitation and inbreeding depression when hermaphrodites are rare. Frequency dependence in several components of the fitness of female and hermaphroditic *Silene vulgaris* was tested in experiments in which the relative numbers of the two sexes was varied among 12 artificial populations. In females, the proportion of flowers that set fruit covaried positively among populations with the frequency of hermaphrodites in two separate experiments, whereas the number of flowers/plant covaried negatively in one case. In hermaphrodites, the number of seeds/fruit covaried positively with the frequency of hermaphrodites, whereas the fitness of hermaphrodites estimated through pollen transfer covaried negatively. The results are discussed as they relate to the selective maintenance of gynodioecy in *S. vulgaris* and in light of a recent model of the effect of population structure on selection in gynodioecious systems.

McCauley, D. E. and M. S. Olson (2003). "Associations among cytoplasmic molecular markers, gender, and components of fitness in *Silene vulgaris*, a gynodioecious plant." *Molecular Ecology* 12(3): 777-787.

cpDNA; fitness; gynodioecy; mtDNA; selection; *Silene*; Caryophyllaceae; selection; breeding system; sex ratio; dimorphism

It has been suggested that the dynamics of chloroplast DNA (cpDNA) or mitochondrial DNA (mtDNA) genetic markers used in studies of plant populations could be influenced by natural selection acting elsewhere in the genome. This could be particularly true in gynodioecious plants if cpDNA or mtDNA genetic markers are in gametic disequilibrium with genes responsible for sex expression. In order to investigate this possibility, a natural population of the gynodioecious plant *Silene vulgaris* was used to study associations among mtDNA haplotype, cpDNA haplotype, sex and some components of fitness through seed. Individuals were sampled for mtDNA and cpDNA haplotype as determined using restriction fragment length polymorphism (RFLP) methods, sex (female or hermaphrodite), fruit number, fruit set, seeds/fruit and seed germination. The sex of surviving germinating seeds was also noted. All individuals in the population fell into one of two cytoplasmic categories, designated haplotypes f and g by a unique electrophoretic signature in both

the mtDNA and cpDNA. The subset of the population carrying haplotype g included a significantly higher proportion of females when compared with the sex ratio of the subset carrying the f haplotype. Haplotype g had a significantly higher fitness when measured by fruit number, fruit set and seeds/fruit, whereas haplotype f had significantly higher fitness when measured by seed germination. Offspring of individuals carrying haplotype g included a significantly greater proportion of females when compared with offspring of individuals carrying the f haplotype. Other studies of gynodioecious plants have shown that females generally have higher fitness through seed than hermaphrodites, but in this study not all fitness differences between haplotypes could be predicted from differences in haplotype-specific sex ratio alone. Rather, some differences in haplotype-specific fitness were due to differences in fitness between individuals of the same sex, but carrying different haplotypes. The results are discussed with regard to the potential for hitchhiking selection to influence the dynamics of the noncoding regions used to designate the cpDNA and mtDNA haplotypes.

McCauley, D. E., J. E. Stevens, et al. (1996). "The spatial distribution of chloroplast DNA and allozyme polymorphisms within a population of *Silene alba* (Caryophyllaceae)." *American Journal of Botany* 83: 727-731.

TW; Caryophyllaceae; *Silene*; ecology; demography; genetics; gene flow; dispersal; Samenausbreitung; pollen; seed; polymorphism; DNA; Chloroplast; allozyme

McNeill, J. and C. W. Crompton (1978). "Pollen dimorphism in *Silene alba* (Caryophyllaceae)." *Canadian Journal of Botany* 56: 1280-1286.

TW; pollen; dimorphism; *Silene*; Caryophyllaceae

Meagher, T. R. (1992). "The quantitative genetics of sexual dimorphism in *Silene latifolia* (Caryophyllaceae) I. Genetic variation." *Evolution* 46: 445-457.

TW; Caryophyllaceae; dimorphism; inflorescence; flower; sex; dioecy; *Silene*; genetics; It is widely recognized that there are basic conflicts between the resource needs of a plant for paternal versus maternal functions. In dioecious species, these divergent demands, and the selection pressures they impose, can lead to the evolution of sexual dimorphism. The present study was conducted to assess the potential for the evolution of sexual dimorphism in *Silene latifolia* by evaluating the genetic variation and genetic correlation between characters and between the sexes for a range of growth and reproductive characters. Sexual dimorphism is largely restricted to reproductive characters, particularly flower number and flower size. A canonical correlation analysis revealed considerable intercorrelation between growth characters, such as germination date, height, and leaf size, and reproductive characters; plants that grow fast early on also flower earlier, and plants that produce big leaves also produce big flowers. There was genetic variation for several sexually dimorphic characters; much of the focus in this analysis was on flower size, particularly calyx diameter. Finally, genetic correlations within and between the sexes were found that limit the rate of evolutionary divergence between the sexes. The genetic results suggest that *S. latifolia* has been subject to divergent selection on the two sexes for a long period of time, bringing about a gradual fixation of sex-limited gene effects, so that the remaining genetic effects are expressed in both sexes. Genetic correlations between the sexes that arise from this residual variation impose limits on further evolutionary change.

Meagher, T. R. (1994). "The quantitative genetics of sexual dimorphism in *Silene latifolia* (Caryophyllaceae) II. Response to sex-specific selection." *Evolution* 48: 939-951.

U; TW; Caryophyllaceae; *Silene*; dimorphism; morphology; genetics; SB; selection; evolution A well-established theoretical relationship exists between genetic correlations between the sexes and the dynamics of response to sex-specific selection. The present study investigates the response to sex-specific selection for two sexually dimorphic traits that have been documented to be genetically variable, calyx diameter and flower number, in *Silene latifolia*. Following the establishment of a base generation with a known genetic background, selection lines were established and two generations of sex-specific selection were imposed. Calyx diameter responded directly to sex-specific selection, and the positive genetic correlation between the sexes was reflected in correlated responses in the sex that was not the basis for selection within a particular line. Flower number showed a more erratic response to sex-specific selection in that selection in some lines was initially in the wrong direction, that is, selection for a decrease in flower number resulted in an increase. These erratic responses were attributable to genotype-environment interaction as reflected in significant heteroscedasticity in variance among families. Correlated responses to selection in the sex that was not the immediate basis for selection indicated the possible existence of a negative genetic correlation between the sexes for this trait. These results

test for the first time the impact of genetic correlations between the sexes on the evolutionary dynamics of sexually dimorphic traits in a plant species.

Meagher, T. R. and D. E. Costich (1994). "Sexual dimorphism in nuclear DNA content and floral morphology in populations of *Silene latifolia* (Caryophyllaceae)." *American Journal of Botany* 81: 1198-1204.

U; TW; morphology; polymorphism; Caryophyllaceae; flower; DNA; sex; *Silene*; floral traits; genetics; differentiation

The evolution of flower size has become a major focus of plant population biology. In order to gain insight into the causal basis for flower-size variation, we have explored the relationship between nuclear DNA content, flower size, and cell size within and among populations of the dioecious plant *Silene latifolia*. We found significant variation among populations for both DNA content and flower size, with a consistent sexual dimorphism within all populations (males have a bigger genome, but smaller flowers). The overall correlation between DNA content and flower size was negative, especially within males. The cell dimensions of calyx and petal cells were not significantly different between the sexes, indicating that females have bigger flowers because they contain more cells. These findings are discussed in the context of nucleotype theory, which predicts a slower growth rate (division rate) for cells with greater DNA content. This leads to the suggestion that males have smaller flowers because of the relatively slow rate of cell division due to their larger genome. It would be of great interest to know whether associated effects on flower size of changes in genome size of the type investigated in the present study can be generalized to other species.

Meagher, T. R. and D. E. Costich (1996). "Nuclear DNA content and floral evolution in *Silene latifolia*."

Proceedings of the Royal Society of London Series B-Biological Sciences 263(1376): 1455-1460.
dimorphism; genetics; gender dimorphism; Caryophyllaceae; sex; dioecy; *Silene*; DNA; evolution; flower

Nuclear DNA content shows extensive intraspecific variation in plants, attributable to changes in levels of repetitive DNA. Since its discovery, repetitive DNA often has been regarded as 'junk' or selfish DNA with little or no evolutionary significance at the individual level, except possibly a deleterious role stemming from its over-replication. However, recent works have pointed out that repetitive DNA may have an important impact on phenotypic selection through local or general modifications of gene expression. Phenotypic evolution has typically been studied using quantitative genetic techniques that treat underlying genetic effects as variance components. In previous work, we identified an among population negative correlation between nuclear DNA content variation, attributable to repetitive DNA, and calyx diameter, a phenotypic character with obvious ecological importance, in *Silene latifolia*. In the present study, we established a negative genetic relation between an AT-biased flow cytometric measure of nuclear DNA content and calyx diameter across lineages that had been subjected to selection for increases or decreases in calyx diameter. This finding suggests that new attention should be directed toward repetitive DNA as a basis for phenotypic variation and evolution.

Meagher, T. R. and L. F. Delph (1996). "Individual flower demography, floral phenology, and life history in *Silene latifolia*." *Bulletin of the Ecological Society of America* 77(3. Suppl., Part 2): 299.

Silene; Caryophyllaceae; flower; floral traits; demography; flowering phenology; anthesis

Meagher, T. R. and L. F. Delph (2001). "Individual flower demography, floral phenology and floral display size in *Silene latifolia*." *Evolutionary Ecology Research* 3(7): 845-860.

U; TW; *Silene*; Caryophyllaceae; demography; flowering phenology; size; flower; floral traits; attractiveness

Flowers, as repeated modules on a plant, may show population dynamics that correspond to ecological models for population growth. We hypothesized that rate of flower production (birth rate), number of open flowers per day (population size) and flower duration (longevity) should be related to plant resource status. With dioecious species, resource demands of male or female function would contribute to sex-specific floral demographics. For example, fruit production in females imposes a resource cost that is absent in males. We recorded individual flower dynamics for 1200 flowers on 85 female plants and 11,179 flowers on 94 male plants in the dioecious species *Silene latifolia*. For males, resource availability was manipulated by defoliating a subset of plants (1587 flowers on 18 plants). For females, resource availability and usage was manipulated as follows: 0% pollinated (401 flowers on 16 plants), 50% pollinated (118 non-pollinated and 131 pollinated flowers on 17 plants), 100% pollinated (470 flowers on 46 plants) and 100% pollinated and defoliated (80 flowers on 6 plants). Populations of flowers on individual plants showed a good fit to the logistic population growth model. Estimated carrying capacities for flowers decrease with decreasing resource availability (males>defoliated males>0% pollinated females>50% pollinated females>100%

pollinated females > 100% pollinated and defoliated females). Pollinated flowers had shorter longevity than non-pollinated flowers. Non-pollinated flowers on plants with 50% pollination had shorter longevity than non-pollinated flowers on plants with 0% pollination. Thus, flower population dynamics within plants do show evidence of resource-based dynamics.

- Melzheimer, V. (1977). "Biosystematische Revision einiger *Silene*-Arten (Caryophyllaceae) der Balkanhalbinsel (Griechenland)." *Botanische Jahrbücher der Systematik* 98: 1-92.
systematics; taxonomy; *Silene*; mediterranean; Griechenland; Europe; Caryophyllaceae; inflorescence; flower; morphology; anatomy; hybrid; TW
- Melzheimer, V. (1980). "Revision einiger balkanischer Arten von *Silene* sect. *Inflatae* (Caryophyllaceae)." *Botanische Jahrbücher der Systematik* 101(2): 153-190.
TW; monography; systematics; taxonomy; *Silene*; Caryophyllaceae; Griechenland
- Melzheimer, V. (1981). "Zum Polymorphismus von *Silene italica* (Caryophyllaceae) im Süd-Balkan." *Botanische Jahrbücher der Systematik* 102(1-4): 285-295.
TW; *Silene*; Caryophyllaceae; demography; morphology; flower; Polymorphism
- Melzheimer, V. (1987). "On the taxonomic position of *Silene thebana* (Caryophyllaceae)." *Plant Systematics and Evolution* 155: 251-256.
TW; Griechenland; Europe; taxonomy; systematics; *Silene*; Caryophyllaceae
- Melzheimer, V. and J. Damboldt (1973). "Zur Morphologie und Cytologie tetraploider Sippen von *Silene vulgaris* (Caryophyllaceae)." *Willdenowia* 7: 83-100.
morphology; Zytologie; molecular biology; systematics; taxonomy; *Silene*; Caryophyllaceae; Polyploidie; TW
- Menges, E. S. (1995). "Factors limiting fecundity and germination in small populations of *Silene regia* (Caryophyllaceae), a rare hummingbird-pollinated Prairie Forb." *American Midland Naturalist* 133(2): 242-255.
Silene; Caryophyllaceae; North America; breeding system; mating system; Ornithophily; GERMINATION; seed; fitness
The prairie forb *Silene regia* is restricted to small isolated populations in the eastern part of its range. I examined factors that limit fecundity and germination in these small populations. Although *S. regia* flowers rarely self due to dichogamy, geitonogamous crosses demonstrated self-compatibility. Substantial fruit production required pollination by ruby-throated hummingbirds (*Archilochus colubris*). Exclusion of hummingbirds (but not most insects) sharply reduced fruit production and seed numbers. Resource competition within individual inflorescences limited percent fruit set in some populations in certain years. Clipping of neighboring vegetation and watering *S. regia* did not increase reproductive output significantly. *Silene regia* seedlings emerged at low rates (15%) in field experiments, but field emergence increased two- to three-fold with soil disturbance and burning. Natural recruitment of seedlings occurred only in burned sites. Of all factors examined, burning had the greatest positive effects on reproductive output. In addition, controlling for the effects of burning, reproductive output was greater for plants in larger than smaller populations. By increasing fecundity and recruitment, prescribed burning can be used to expand population sizes of *Silene regia*.
- Menges, E. S. and R. W. Dolan (1998). "Demographic viability of populations of *Silene regia* in midwestern prairies - relationships with fire management, genetic variation, geographic location, population size and isolation." *Journal of Ecology* 86(1): 63-78.
TW; habitat; fragmentation; population; size; viability; USA; North America; Prairie; *Silene*; Caryophyllaceae; ecology; demography; biogeography; disturbance; fire; extinction; grassland; disturbance
1 We studied the demographic viability of populations of a long-lived iteroparous prairie perennial, *Silene regia*, in relation to management regimes, population sizes, geographical region (Ohio and Indiana vs. Missouri and Arkansas), degree of isolation and amount of genetic variation. Demographic data were collected from 16 populations for up to 7 years. 2 This species has high survivorship, slow growth, frequent flowering and episodic seedling recruitment. Matrix projection methods were used to summarize population performance with and without recruitment. Median finite rates of increase by population varied from 0.57 to 1.82 and from 0.44 to 0.99, respectively. 3 Populations with the highest rates of increase had been burned. Six of eight populations, for which stochastic modelling predicted persistence for 1000 years, included fire in their management. None

of the five populations with predicted 100-year extinction probabilities of 100% was managed for conservation or burned. An intermediate group of three populations with at least 10% probability of extinction between 100 and 1000 years was not managed, but was none the less kept open by mowing and herbicide application. 4 Analysis of composite elasticities showed that growth and fecundity terms were higher for growing (vs. Declining) populations and that growth elasticity was higher in burned than unburned populations. Lack of burning shifts the elasticity spectrum from that typical of open habitat herbs (higher growth and fecundity elasticities) to values usually found for closed habitat herbs (higher survival elasticities). 5 In multivariate analyses predicting finite rates of increase (with and without recruitment), fire management and region were the strongest predictors, followed by genetic variation, population size, isolation and interactions of population size and fire, and region and fire. Populations with the highest rates of increase were burned, eastern, more genetically diverse, larger and less isolated. Discrimination of populations with different extinction risks (three classes) was related mainly to fire, genetic variation and region. 6 Most of these conclusions support conservation biology predictions that population viability will be highest in larger, less-isolated, more genetically diverse populations. However, management and geographic trends have overriding roles affecting demographic viability. Habitat fragmentation and genetic depletion have the potential to threaten residual prairie populations of *S. regia*, but lack of fire management appears to be the primary short-term threat.

Mengoni, A., C. Gonnelli, et al. (2000). "Genetic diversity and heavy metal tolerance in populations of *Silene paradoxa* L. (Caryophyllaceae) - a random amplified polymorphic DNA analysis." *Molecular Ecology* 9: 1319-1324.

TW; RAPD; genetics; molecular biology; demography; *Silene*; Caryophyllaceae; heavy metal

Mengoni, A., C. Gonnelli, et al. (2003). "Evolution of copper-tolerance and increased expression of a 2b-type metallothionein gene in *Silene paradoxa* L. populations." *Plant and Soil* 257(2): 451-457.

heavy metal; evolution; *Silene*; Caryophyllaceae; evolution; ecology; adaptation

Two independently evolved cupricolous populations, their ancestral serpentine population, another unrelated serpentine population and a non-metallicolous population of *Silene paradoxa* L. were compared for copper tolerance and foliar transcript levels of a 2b-type metallothionein gene that was previously shown to be involved in copper tolerance in the congener, *S. vulgaris*. The levels of copper tolerance and constitutive MT2b expression, assessed by Northern-blot analysis and semiquantitative RT-PCR, were proportionally increased in the cupricolous populations, as compared to the serpentine and the non-metallicolous populations. Southern-blot analysis revealed amplification of the gene in the cupricolous populations, such as in *S. vulgaris*, which might account for the higher constitutive expression level. Since the cupricolous populations descended separately from a common serpentine ancestral population, these results imply that MT2b overexpression must have been independently evolved in both of them, again such as previously shown *S. vulgaris*. Thus, both in *S. paradoxa* and *S. vulgaris*, the MT2b locus appears to be a major target for natural selection imposed by soil copper toxicity.

Meyhöfer, R. (1998). "Pflanze, Pilz, Bestäuber - Ménage à trois mit Folgen." *Sekundarstufe II* 22: 44-48.

TW; pollination; Mycophyta; interaction; *Silene*; Caryophyllaceae

Miller Alexander, H. (1987). "Pollination limitation in a population of *Silene alba* infected by the anther-smut fungus *Ustilago violacea*." *Journal of Ecology* 75(3): 771-780.

pollination; Caryophyllaceae; *Silene*; anther smut; *Ustilago violacea*;

(1) In a population of *Silene alba*, female plants where all flowers had been hand-pollinated had more than double the proportion of flowers maturing fruit and number of seeds per fruit compared with control plants, suggesting pollination limitation. (2) Hand-pollinated and control plants produced the same number of fruits over the season because hand-pollinated plants produced a smaller total number of flowers, apparently due to limited availability of resources such as energy, water or nutrients. (3) Thirty per cent of the flowering plants in the population produced sterile, spore-producing flowers because of infection by the anther-smut fungus *Ustilago violacea*; infection can occur following pollinator transport of spores. Eight of the thirty plants in the experiment became infected by *U. violacea* late in the season; six of these were control plants. Plants that became infected had produced significantly more flowers over the season than plants that remained disease-free.

Miller Alexander, H. (1990). "Epidemiology of anther-smut infection of *Silene alba* caused by *Ustilago violacea*: Patterns of spore deposition and disease incidence." *Journal of Ecology* 78: 166-179.

Silene; Caryophyllaceae; Mycophyta; interaction; dispersal; demography; TW; parasitism; spores; infection; dispersal

Miller Alexander, H. (1990). "Anther-smut infection of *Silene alba* caused by *Ustilago violacea*: factors determining fungal reproduction." *Oecologia* 84: 249-253.

Silene; Caryophyllaceae; Ustilaginales; Mycophyta; TW; parasitism; INFECTION

Miller Alexander, H. and J. Antonivics (1988). "Disease spread and population dynamics of anther-smut infection of *Silene alba* caused by the fungus *Ustilago violacea*." *Journal of Ecology* 76: 91-104.

Ustilaginales; *Silene*; Caryophyllaceae; demography; Mycophyta; TW; parasitism; spores; infection; dispersal; pathogen; interaction

Moneger, F. (2001). "Molecular and evolutionary analysis of a plant Y chromosome." *Comptes Rendus De L Academie Des Sciences Serie Iii-Sciences De La Vie-Life Sciences* 324(6): 531-535.

Plants have evolved a great diversity of sex determination systems. Among these, the XY system, also found in mammals, is one of the most exciting since it gives the opportunity to compare the evolution of sex chromosomes in two different kingdoms. Whereas generic and molecular mechanisms controlling sex determination in *Drosophila* and mammals, have been well studied, very little is known about such processes in plants. White campion (*Silene latifolia*) is an example of plant with X and Y chromosomes. What is the origin of the X and Y chromosomes! How did they evolve from a pair of autosomes! In our laboratory, we have isolated the first active genes located on a plant Y chromosome. We are using them as markers to trace the origin and evolution of sex chromosomes in the *Silene* genus. (C) 2001 Academie des sciences/Editions scientifiques et medicales Elsevier SAS.

Moneger, F., N. Barbacar, et al. (2000). "Dioecious *Silene* at the X-road: the reasons Y." *Sexual Plant Reproduction* 12(4): 245-249.

U; TW; dioecy; *Silene*; Caryophyllaceae; sexual system; sex; chromosomes; evolution; genetics; gene; karyology

Among the variety of breeding systems developed by flowering plants, those based on heteromorphic sex chromosomes are the most intellectually challenging in evolutionary terms. This is because, among other things, they enable us to compare sex determination processes between plants and animals. White campion (*Silene latifolia*, also named *Lychnis* or *Melandrium*) is dioecious and, much like us, females are homogametic (XX) and males are heterogametic (XY). Sexual dimorphism in white campion is controlled by two independent developmental pathways operating from the Y chromosome at very early developmental stages and within distinct regions of the flower. In addition, all basic steps in the evolution from the bisexual to the dioecious condition with heteromorphic sex chromosomes are known and available to experimentation in the genus *Silene*. This group of species has been under scrutiny for more than a century. Such an ideal experimental system enables us to tackle, with novel methodological tools, several classical questions in biology. These include the question of how sexual dimorphism evolved and how dimorphic development is controlled, as well as questions of how sex chromosomes evolve in the absence of meiotic recombination or how male-female genetic conflicts are generated. At the turn of the century, the time is now ripe to have a closer look.

Moore, R. C., O. Kozyreva, et al. (2003). "Genetic and functional analysis of DD44, a sex-linked gene from the dioecious plant *Silene latifolia*, provides clues to early events in sex chromosome evolution." *Genetics* 163(1): 321-334.

evolution; PCR; *Silene*; Caryophyllaceae; sex; chromosomes; gene; dioecy; genetics

Silene latifolia is a dioecious plant with heteromorphic sex chromosomes. The sex chromosomes of *S. latifolia* provide an opportunity to study the early events in sex chromosome evolution because of their relatively recent emergence. In this article, we present the genetic and physical mapping, expression analysis, and molecular evolutionary analysis of a sex-linked gene from *S. latifolia*, DD44 (Differential Display 44). DD44 is homologous to the oligomycin sensitivity-conferring protein, an essential component of the mitochondrial ATP synthase, and is ubiquitously expressed in both sexes. We have been able to genetically map DD44 to a region of the Y chromosome that is genetically linked to the carpel-suppressing locus. Although we have physically mapped DD44 to the distal end of the long arm of the X chromosome using fluorescence in situ hybridization (FISH), DD44 maps to the opposite arm of the Y chromosome as determined by our genetic map. These data suggest that chromosomal rearrangements have occurred on the Y chromosome, which may have contributed to the genetic isolation of the Y chromosome. We discuss the implications of these results with respect to the structural and functional evolution of the *S. latifolia* Y chromosome.

- Mörchen, G. (1972). "Über den unterschiedlichen Wuchs zweier einheimischer Lichtnelken." *Hercynia* 9: 271-274.
TW; *Silene*; Caryophyllaceae; growth; life form; Europe; Germany
- Morriset, P. (1966). "Tetraploid *Silene vulgaris* (Moench) Garcke in Europe." *Proceedings of the Botanical Society of the British Isles*: 278-279.
Silene; Polyploidie; genetics; Caryophyllaceae; Europe; TW
- Morris, W. F. and D. F. Doak (1998). "Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices." *American Journal of Botany* 85(6): 784-793.
TW; alpine; Caryophyllaceae; gynodioecy; life history; evolution; selection; demography; success; dioecy; *Silene*; pollination; autecology; sex; gynodioecy; EM
Alpine plants often appear to have long life-spans as an adaptation to harsh and unpredictable environmental conditions, yet many lack reliable indicators of age that would make it possible to determine their true longevity. Their extended lifespans also pose problems for measuring lifetime reproductive success, a key component of breeding system evolution in species such as the gynodioecious cushion plant *Silene acaulis*. For a population of *S. acaulis* in south-central Alaska, we applied a recently derived analytical approach using size-based population projection matrices that allowed us to estimate: (1) the relationship between cushion diameter and age; and (2) lifetime reproductive success through seed production by females relative to hermaphrodites. Because of a combination of slow growth, frequent shrinkage, and extremely high adult survival, we estimate that the largest cushions in our study population exceed 300 yr in age, and some may live substantially longer, despite the seemingly inhospitable alpine environment they inhabit. Females are estimated to produce 4.4 times as many offspring via seed production over the course of their lives as do hermaphrodites, a difference that is more than sufficient to assure the persistence of females despite their inability to transmit genes through pollen. These results highlight the utility of size-based projection matrices for studying the life histories of herbaceous perennials whose life-span and lifetime reproductive success cannot be determined easily by any other means.
- Mulcahy, D. L. (1967). "Optimal sex ratio in *Silene alba*." *Heredity* 22: 411-423.
EM; breeding system; sex; Caryophyllaceae; *Silene*; sexual system; pollen; competition; TW; sex ratio
- Mulcahy, D. L. (1968). "The significance of delayed pistillate anthesis in *Silene alba*." *Bulletin of the Torrey Botanical Club* 95: 135-139.
anthesis; flowering phenology; flower; reproduction; *Silene*; Caryophyllaceae; TW
- Mustajarvi, K., P. Siikamaki, et al. (2001). "Consequences of plant population size and density for plant-pollinator interactions and plant performance." *Journal of Ecology* 89(1): 80-87.
TW; pollinator behavior; interaction; Geitonogamie; Fragmentation; *Lychnis*; Caryophyllaceae; demography; pollination
1 Habitat fragmentation and the resulting decline in the local abundance of plant species can affect biological interactions. We examined the effects of abundance on plant-pollinator interactions by observing the pollinator service and subsequent reproductive output of a mostly outbreeding, but self-compatible, plant, *Lychnis viscaria*, in experimental populations of different sizes (number of individuals) and densities (distance between individuals). 2 Bumblebees, the main pollinators of *L. viscaria*, preferred larger populations, but visitation rates were higher in sparser populations. Pollinators were attracted to the larger inflorescences in sparse populations, which were also more visible due to their larger area for a given size. 3 Bumblebees probed more flowers within plants in sparse populations, probably due to the larger inflorescences and longer flight distances between individuals. 4 Subsequent reproductive success (capsule production) was higher in sparse populations, due to differences in pollination success and resource competition, and their interaction. In self-compatible species, such as *L. viscaria*, reproductive success may be determined more by resource availability, whereas self-incompatible plants may be more sensitive to changes in pollinator abundance. 5 We conclude that plant-pollinator interactions are sensitive to changes in both the size and spatial arrangement of plant populations, which can affect their demography and genetics. In this study, species density had a greater effect than size and the unexpectedly beneficial effects of low density may be due to greater resource availability.

- Neumayer, H. (1923). "Einige Fragen der speziellen Systematik, erläutert an einer Gruppe der Gattung *Silene*." Österreichische Botanische Zeitschrift 72: 276-287.
TW; *Silene*; Caryophyllaceae; systematics; taxonomy
- Nielsen, A. and R. A. Ims (2000). "Bumble bee pollination of the sticky catchfly in a fragmented agricultural landscape." *Ecoscience* 7(2): 157-165.
U; TW; *Bombus*; pollination; fragmentation; patterns; *Silene*; Caryophyllaceae; seed set; habitat; melittophily; pollen limitation; pollinator behavior; population; agriculture; disturbance
Seed set and pollinator activity of bumble bees were examined in a fragmented population of sticky catchfly (*Viscaria vulgaris*). We focused on the potential effect of the spatial distribution of plant individuals at three hierarchical levels: islet level (outcrops with seminatural vegetation in the agricultural fields), patch level (aggregations of plant individuals within islets), and tussock level (plant individuals within patches). Size of patches and islets were study design parameters, whereas isolation at the patch and islet level and size at the tussock level were treated in the analysis as covariates. Isolation of islets and patches had no significant effect on the response variables (seed set and bumble bee activity). However, the isolation of islets and patches was quite small compared to the activity range of bumble bees in the study area. While islet size seemed to be unimportant, both pollinator activity and seed set increased with increasing patch and tussock size, whereas the frequency of aborted seeds decreased. The increased seed set of larger and presumably older patches and tussocks indicate that to maximize viability of a fragmented, perennial herb population, it is important to minimize local disturbance so that individual subpopulations may develop over time.
- Nougarède, A., D. Francis, et al. (1993). "Floral events in *Silene coeli-rosa*." *Acta Botanica Gallica* 140: 659-684.
flower; Caryophyllaceae; physiology; phenology; *Silene*; TW; anthesis
- Oberdorfer, E. Caryophyllales. In: 371.
Caryophyllaceae; key; *Silene*; TW
- Olson, M. S. and D. E. McCauley (2002). "Mitochondrial DNA diversity, population structure, and gender association in the gynodioecious plant *Silene vulgaris*." *Evolution* 56(2): 253-262.
Caryophyllaceae; gene flow; genetic structure; DNA; seed dispersal; sex ratio; *Silene*; RFLP; gynodioecy; population
A highly variable mitochondrial DNA (mtDNA) restriction fragment length polymorphism (RFLP) locus is used to assess the population structure of mitochondrial genomes in the gynodioecious plant *Silene vulgaris* at two spatial scales. Thirteen mtDNA haplotypes were identified within 250 individuals from 18 populations in a 20-km diameter region of western Virginia. The population structure of these mtDNA haplotypes was estimated as $\theta(ST) = 0.574$ (± 0.066 SE) and, surprisingly, genetic differentiation among populations was negatively correlated with geographic distance (Mantel $r = -0.246$, $P < 0.002$). Additionally, mtDNA haplotypes were spatially clumped at the scale of meters within one population. Gender in *S. vulgaris* is determined by an interaction between autosomal male fertility restorers and cytoplasmic male sterility (CMS) factors, and seed fitness is affected by an interaction between gender and population sex ration thus, selection acting on gender could influence the distribution of mtDNA RFLP haplotypes. The sex ratio (females: hermaphrodites) varied among mtDNA haplotypes across the entire meta- population, possibly because the haplotypes were in linkage disequilibrium with different CMS factors. The gender associated with some of the most common haplotypes varied among populations, suggesting that there is also population structure in male fertility restorer genes. In comparison with reports of mtDNA variation from other published studies, we found that *S. vulgaris* exhibits a large number of mtDNA haplotypes relative to that observed in other species.
- Ouborg, N. J., A. Biere, et al. (2000). "Inbreeding effects on resistance and transmission-related traits in the *Silene-Microbotryum* pathosystem." *Ecology* 81(2): 520-531.
U; TW; inbreeding; *Silene*; Caryophyllaceae; Ustilaginales; parasitism; pathogen; interaction
Inbreeding in local host populations will be a common phenomenon in host-pathogen systems that are characterized by metapopulation dynamics, i.e., frequent extinction and recolonization of local host populations by small numbers of founding individuals. As an example of a pathosystem with metapopulation dynamics we investigated the impact of inbreeding in the host plant *Silene alba* on its interaction with the anther-smut fungus *Microbotryum violaceum*. Seeds from eight populations of *S. alba* were sampled, and five generations of sib mating resulted in 65 inbred lines, with inbreeding coefficients of $f = 0, 0.25, 0.375, 0.5, \text{ and } 0.59$ per line. In a first experiment these lines were tested

for active, biochemical resistance against fungal infection, by artificially inoculating individuals. The percentage of infected individuals differed significantly among populations, lines, and inbreeding levels, and both population-by-inbreeding level and line-by-inbreeding level interactions were significant. The most striking result was the strong variance in inbreeding effects among lines; inbreeding resulted in increased resistance in some lines and decreased resistance in others. In a second experiment for 12 inbred lines, originating from one population, active resistance and Rower traits associated with passive resistance (avoidance) to this insect- vectored, florally transmitted disease were measured. Significant inbreeding depression was demonstrated for petal size and nectar volume. Thus inbreeding might enhance avoidance of spore transmission by insects. For both active resistance and all flower traits, significant line-by-inbreeding level interactions were found. The results indicate that the effect of inbreeding on the interaction between host and pathogen in this pathosystem is unpredictable at the local population level, because: (1) strong genotypic differences in inbreeding effect exist for both active and passive resistance, making the effect of inbreeding at the population level dependent on the genotypic composition of the (founder) population (2) effects of inbreeding on active and passive resistance were not correlated, making the net effect of inbreeding on field resistance unpredictable: and (3) in several lines, evidence for epistatic effects was found, making the effect of inbreeding dependent on the actual inbreeding level of the genotype. The results underscore that most progress in the study of host-path from an integrated ecological and genetic approach.

- Oxelman, B. (1996). "RAPD patterns, nrDNA ITS sequences and morphological patterns in *Silene* section Sedoideae (Caryophyllaceae)." *Plant Systematics and Evolution* 201: 93-116.
RAPD; DNA; morphology; *Silene*; Caryophyllaceae; systematics; evolution; taxonomy; AJ; TW; phylogeny
Hierarchical patterns in *Silene* sect. Sedoideae were investigated using random amplified polymorphic DNA (RAPD), nucleotide sequences of the internal transcribed spacer (ITS) regions of the 18S-28S nuclear ribosomal DNA, and discrete morphological characters. All data sets firmly supported the species recognized. The RAPD data offered the best resolution at the intraspecific level, supporting the current intraspecific classifications of *S. sedoides* and *S. integripetala*. The ITS sequences and the morphological data gave poor resolution within species, and the three data sets disagreed about the relationships among species. The signal from the RAPD data was strongest and remained when the total data set was analysed. The three data sets all support an amphiploid origin of *S. aegaea*, with the strongest evidence from the ITS sequences. Incongruences among data sets as well as merits and shortcomings of each are discussed. The robustness of the results can be evaluated using perturbations of data, i.e., bootstrap and jackknife of taxa and characters. These methods should not be taken as methods of statistical inference at the taxonomic level, because unbiased sampling appears impossible. RAPD data, however, come close to being suitable for statistical estimation of hierarchies at the genome level, but several methodological problems have to be solved.
- Oxelman, B. and M. Liden (1995). "Generic boundaries in the tribe *Sileneae* (Caryophyllaceae) as inferred from nuclear rDNA sequences." *Taxon* 44(4): 525-542.
genetics; molecular biology; systematics; taxonomy; *Silene*; Caryophyllaceae; DNA; EM; TW
The relationships within the tribe *Sileneae* (Caryophyllaceae, Caryophylloideae) were deduced from nucleotide sequence variation in the nuclear ribosomal DNA. The internal transcribed spacer (ITS) regions and the intervening 5.8S gene were sequenced for 76 ingroup and five outgroup taxa. The relationships were analysed more closely for 26 of these, with the addition of 822 aligned positions from the 28S gene. *Drypis* appears not to belong in *Sileneae*, and perhaps not even in Caryophylloideae. *Agrostemma* is sister group to the rest of the tribe. *Eudianthe* (*Silene coeli-rosa* and *S. laeta*) and *Petrocoptis* are clearly separated from the core *Silene*. *Steris* (*Viscaria*) *Silene* sect. *Heliosperma*, sect. *Rupifraga*, and sect. *Compactae* together form a strongly supported clade, as do *Lychnis* plus *Uebelina*. *Cucubalus*, *Melandrium*, and *Gastrolychnis* are nested within a weakly supported "*Silene*": *Polyschemone*, previously often misplaced in *Lychnis*, is apparently closely related to *Silene acaulis*. Within the core *Silene*, three main groups can be identified, corresponding roughly to three of Rohrbach's (1869) five main generic subdivisions, *S. subg. Behen*, sect. *Cincinnosilene*, and sect. *Botryosilene*. *Pleconax* *Melandrium*, *Cucubalus*, and *Gastrolychnis* nest within *S. subg. Behen*, but the monophyly of this group is weakly supported. Members of *S. sect. Dichasiosilene* are scattered over all three groups, indicating that dichasium is plesiomorphic within the group.
- Oxelman, B., M. Lidén, et al. (1997). "Chloroplast rps16 intron phylogeny of the tribe *Sileneae* (Caryophyllaceae)." *Plant Systematics and Evolution* 206: 393-410.

TW; Chloroplast; DNA; genetics; genetics; molecular biology; Caryophyllaceae; *Silene*; *Lychnis*; evolution; ITS; systematics; rps; plastid; phylogeny

Intron sequences of the chloroplast gene rps16 from 46 species were used to examine phylogenetic relationships indicated by nrDNA ITS sequence variation in the tribe *Sileneae* (Caryophyllaceae, Caryophylloideae). This region has previously not been utilized for phylogenetic purposes but the results presented here suggest that it is a consistent and valuable complement to the ITS sequences. The rps16 intron trees are largely congruent with the ITS trees. All the major hypotheses suggested by the ITS data are supported, often at similar bootstrap levels. The joint usage of rps16 intron and ITS sequences provides a powerful tool for resolving many of the difficult taxonomic issues in the tribe *Sileneae*.

Oxelman, B., M. Liden, et al. (2001). "Taxonomic and nomenclatural notes on Chinese *Silene* (Caryophyllaceae)." *Novon* 11(3): 322-324.

Caryophyllaceae; China; *Silene*

A revision of the Chinese species of *Silene* L. for the forthcoming account of that genus in the Flora of China, Volume 6, necessitates publication of the following two new combinations, one new rank, one replacement name., and three new species: *Silene davidii* (Franchet) Oxelman & Liden, comb. nov., *S. kialensis* (F. N. Williams) Liden & Oxelman, comb. nov., *S. herbilegorum* (Boequet) Liden & Oxelman, stat. nov., *S. principis* Oxelman & Liden, nom. nov., *S. sveae* Liden & Oxelman, sp. nov., *S. tubulosa* Oxelman & Liden, sp. nov., and *S. tibetica* Liden & Oxelman, sp. nov.

Peschken, D. P., R. DeclerckFloate, et al. (1997). "*Cassida azurea* Fab. (Coleoptera, Chrysomelidae) Host specificity and establishment in Canada as a biological control agent against the weed *Silene vulgaris* (Moench) Garcke." *Canadian Entomologist* 129(5): 949-958.

TW; *Silene*; Caryophyllaceae; interaction; herbivory; Canada; conservation biology

Cassida azurea Fab. (Coleoptera: Chrysomelidae) was studied as an agent to control the weed bladder campion, *Silene vulgaris* (Moench) Garcke (Caryophyllaceae). To supplement previously published data on the beetle's host range, additional no-choice experiments were conducted. First-stage larvae were offered seven plant species related to bladder campion. Only one adult male developed on *Dianthus caryophyllus* L. Cv. China Doll and one female on *Lychnis X haageana* Lem. This female did not produce eggs when it continued to feed on L. X haageana. In tests with adults, oogenesis occurred only if fed with bladder campion, and one laid one egg while feeding on *Gypsophila pacifica* Kom. First-stage larvae did not develop to adults on three native North American *Silene* spp., but two adults developed on three other native species. Based on results from these experiments and reports in the literature, it was concluded that *C. azurea* has a very narrow host range and permission for field releases was granted in 1989. Releases were made in Manitoba, Saskatchewan, and Alberta from 1989 to 1993. *Cassida azurea* survived from 3 to 6 years and was considered established at 8 of the 18 release sites in the three provinces but has not yet increased to densities sufficient to reduce bladder campion populations.

Pettersson, M. W. (1991). "Flower herbivory and seed predation in *Silene vulgaris* (Caryophyllaceae) - effects of pollination and phenology." *Holarctic Ecology* 14: 45-50.

pe; fam; moths; Caryophyllaceae; *Silene*; predation; pollination; phenology; herbivory; Noctuidae; TW; parasitism

Pettersson, M. W. (1991). "Pollination by a guild of fluctuating moth populations - Option for unspecialization in *Silene vulgaris*." *Journal of Ecology* 79: 591-604.

pe; Lepidoptera; generalistic; efficiency; moths; *Silene*; Caryophyllaceae; sphingophily; pollination; Noctuidae; TW

Pettersson, M. W. (1992). "Pollination, oviposition and seed predation by flower visiting insects in bladder campions (*Silene vulgaris* S.L., Caryophyllaceae)." *Acta Universitatis Upsaliensis* 399: 1-32.

moths; sphingophily; predation; pollination; Caryophyllaceae; *Silene*; Noctuidae; TW; seed predation

Pettersson, M. W. (1992). "Advantages of being a specialist female in the gynodioecious *Silene vulgaris* s.l. (Caryophyllaceae)." *American Journal of Botany* 79: 1389-1395.

pe; gynodioecy; seed survival; seed; EM; gynodioecy; Caryophyllaceae; *Silene*; sex; seed set; Sweden; Europe; TW; breeding system

Pettersson, M. W. (1992). "Density-dependent egg dispersion in flowers of *Silene vulgaris* by the seed predator *Hadena confusa* (Noctuidae)." *Ecological Entomology* 17: 244-248.

pe; an; moths; sphingophily; Lepidoptera; Caryophyllaceae; *Silene*; Ovar; predation; pollinator behavior; Schweden; Europe; Noctuidae; TW; seed predation

Pettersson, M. W. (1992). "Taking a chance on moths: Oviposition by *Delia flavifrons* (Diptera Anthomyiidae) on the flowers of bladder campion, *Silene vulgaris* (Caryophyllaceae)." *Ecological Entomology* 17: 57-62.

moths; Ovar; Diptera; *Silene*; Caryophyllaceae; pollination; predation; Noctuidae; TW; seed predation; phalaenophily; Lepidoptera

Pettersson, M. W. (1994). "Large plant size counteracts early seed predation during the extended flowering season of a *Silene uniflora* (Caryophyllaceae) population." *Ecography* 17: 264-271.

Hadena; Caryophyllaceae; TW; *Silene*; phenology; evolution; seed; predation; seed bank; Noctuidae; SB; seed predation; interaction; display; growth; pollination; phalaenophily

Pettersson, M. W. (1997). "Solitary plants do as well as clumped ones in *Silene uniflora* (Caryophyllaceae)." *Ecography* 20(4): 375-382.

reproductive success; population; density; size; xenogamy; breeding system; efficiency; TW; EM; pollination; predation; floral traits; demography; gynodioecy; Caryophyllaceae; *Silene*
Many studies have been done on seed production as a function of population density in wild plants. Most of them show a higher seed-set per flower of densely growing plants. In this study, in a gynodioecious *Silene uniflora* (Caryophyllaceae) population on the Baltic island of Gland, high plant density did not increase fruit-set or seed-set. Instead, the total number of seeds set was slightly higher for widely scattered plants as a result of a somewhat lower number of ovules per flower in densely growing plants. Individuals had nothing to gain by growing close together, because there was no reproductive parameter which could compensate for the low ovule number per flower of closely growing plants. Plant size determined the total seed production of individuals, but did not correlate with any of the fitness components studied per flower basis. The different gender morphs showed the same pattern, which is discussed as a comparison with pollen limitation in self-compatible and self-incompatible plants.

Popp, M. and B. Oxelman (2001). "Inferring the history of the polyploid *Silene aegaea* (Caryophyllaceae) using plastid and homoeologous nuclear DNA sequences." *Molecular Phylogenetics and Evolution* 20(3): 474-481.

Silene; Caryophyllaceae; polyploidy; plastid; DNA; nuclear rDNA; phylogeny; ITS
The origin of the rare allotetraploid *Silene aegaea* was inferred from plastid rps16 intron sequences, homoeologous copies of nuclear ribosomal internal transcribed spacer (ITS) sequences, and an intron from the nuclear gene coding for the second largest subunit of RNA polymerase II (RPB2). The nuclear DNA regions support the *S. sedoides* and *S. pentelica* lineages as most closely related to the two *S. aegaea* paralogues. A few recombinant ITS sequences were found, but as PCR recombination could be demonstrated, no true recombination could be demonstrated. No recombination was found in the RPB2 sequences. Plastid rps16 intron sequences strongly support *S. pentelica* as the maternal lineage. The strength of the approach of using homoeologous sequences of several loci is demonstrated, and its usefulness for the study of phylogenies of groups including polyploids is emphasized. (C) 2001 Academic Press.

Prentice, H. C. (1976). "A study in endemism: *Silene diclinis*." *Biological Conservation* 10(1): 15-30.

TW; endemism; *Silene*; Caryophyllaceae; conservation biology; dioecy; Spain; Europe; distribution;

Prentice, H. C. (1979). "Numerical analysis of infraspecific variation in European *Silene alba* and *S. dioica* (Caryophyllaceae)." *Botanical Journal of the Linnean Society* 78: 181-212.

TW; *Silene*; Caryophyllaceae; Europe; geography; seed; demography

Prentice, H. C. (1984). "The sex ratio in a dioecious endemic plant, *Silene diclinis*." *Genetica* 64: 129-133.

dioecy; sex; reproduction; Endemismus; Spanien; Europe; *Silene*; Caryophyllaceae; genetics; TW

Prentice, H. C., J. U. Malm, et al. (2003). "Allozyme and chloroplast DNA variation in island and mainland populations of the rare Spanish endemic, *Silene hifacensis* (Caryophyllaceae)." *Conservation Genetics* 4(5): 543-555.

allozymes; plastid; DNA; cpDNA; endemism; population; *Silene*; Caryophyllaceae; endemism; Spain; Europe; extinction; variation; genetic diversity; conservation

Silene hifacensis is a narrowly endemic plant, restricted to a few small populations on limestone cliffs in the Spanish province of Alicante and on the Balearic island of Ibiza. The species was

collected to extinction in its original mainland location by the early 20th century. Attempts have been made to reintroduce *S. hifacensis* to this area but conservation efforts are limited by a lack of information on the geographic structure of genetic variation in the species. We used nuclear (allozyme) and chloroplast DNA (cpDNA) PCR/RFLP markers to investigate the structure of genetic variation in 2 mainland and 6 Ibiza populations. Levels of allozyme variation were low, with a mean of 2 alleles per polymorphic locus. Mean (over polymorphic loci) total allozyme diversity ($H\text{-tot}$) was 0.203 and mean within-population diversity ($H\text{-pop}$) was 0.085. Most diversity was explained by the between-population diversity component ($G(\text{pop})_{\text{reg}} = 57\%$). Both mainland populations showed allozyme fixation. Three composite cpDNA haplotypes were identified. The first is unique to a mainland population that is also allozymically distinct from all the other populations. The second haplotype is found in the other mainland population and one Ibiza population: these two populations are allozymically identical. The remaining Ibiza populations contain the third haplotype. The geographic distribution of allozymes and cpDNA haplotypes is discussed in terms of population history, dispersal and, speculatively, in terms of the possibility that there has been undocumented translocation of material between populations.

Prentice, H. C. and O. Mastenbroek (1984). "Geographic variation in the pollen of *Silene latifolia* (*S. alba*, *S. pratensis*): A quantitative morphological analysis of population data." *Canadian Journal of Botany* 62: 1259-1267.

Silene; Caryophyllaceae; Pflanzengeographie; demography; morphology; Europe; Elektronenmikroskopie; TW

Purrington, C. B. (1993). "Parental effects on progeny sex ratio, emergence, and flowering in *Silene latifolia* (Caryophyllaceae)." *Journal of Ecology* 81(4): 807-811.

phenology; Paternity analysis; *Silene*; dioecy; competition; polymorphism; sex; TW; sex ratio
1. The dioecious perennial, *Silene latifolia* (Caryophyllaceae) was tested to determine whether parental nutrient condition and pollination position affects sex ratio, emergence date, and age at first flowering of the progeny. 2. Parental plants were grown under two nutrient regimes (either full-strength or 25% fertilizer). One flower on each female plant was pollinated on the basal portion of the receptive stigmatic lobes, and another on the distal region. Seeds from the mature capsules were grown in the glasshouse until flowering and emergence date, flowering date, and sex were recorded for each individual. 3. Neither the position of pollen application nor the nutrient condition of the parents affected progeny sex ratio. 4. Progeny from low nutrient parents emerged and flowered later than progeny from high nutrient parents. 5. Seeds produced from basal pollinations emerged more slowly than seeds from distal pollinations, suggesting that gametophytic selection affected progeny vigour. 6. Males emerged earlier than females, but flowered at a greater age. The difference in age at flowering between males and females was greater in progeny from low nutrient parents. 7. Parental effects on sexual dimorphism in emergence and maturation time, coupled with sex-specific selection on emergence time and flowering phenology, may thus be important in the population dynamics of this dioecious plant.

Purrington, C. B. and J. Schmitt (1995). "Sexual dimorphism of dormancy and survivorship in buried seeds of *Silene latifolia*." *Journal of Ecology* 83: 795-800.

polymorphism; Samenbank; seed; germination; *Silene*; Caryophyllaceae; dioecy; sex; TW

Richards, C. M. (2000). "Inbreeding depression and genetic rescue in a plant metapopulation." *American Naturalist* 155(3): 383-394.

U; TW; inbreeding; population; gene flow; isolation; evolution; theory

While migration of individuals has been shown to increase the persistence of small isolated populations through a process known as the "rescue effect," the demographic effects that pollen-mediated gene flow may have in plant populations are not known empirically. This study investigates the role that inbreeding depression plays in newly colonized populations of a common, dioecious, weedy species, *Silene alba*. Experimental greenhouse studies presented here show that *S. alba* displays high levels of inbreeding depression (expressed as lowered germination success) in progeny produced with inbreeding coefficients of 0.125 (half-sib mated), 0.250 (full-sib mated), and 0.375 (second-generation sib mated). In addition, it is shown that the degree of inbreeding depression in 12 natural colonies varies with the degree of isolation from other established populations. Significantly, data from experimental populations showed that gene flow into patches comprised of full sibs was higher than those observed into patches comprised of unrelated individuals and may serve to mitigate the effects of inbreeding depression. It is suggested that population connectivity through pollen-mediated gene flow may have substantial effects on the persistence of isolated colonies and on the spatial structure of a metapopulation in general.

Richards, C. M., S. Church, et al. (1999). "The influence of population size and isolation on gene flow by pollen in *Silene alba*." *Evolution* 53(1): 63-73.

U; TW; colonization; gene flow; population; genetics; pollen; dispersal; *Silene*; pollination; Caryophyllaceae; Reproduction; demography; Isolation; experiment

In a series of experiments conducted over two seasons, we used arrays of experimental populations to examine the effects of flower number and distance between patches on gene flow by pollen. For this study we used the dioecious, short-lived perennial plant *Silene alba* (Caryophyllaceae). This species lives in disturbed roadside and agricultural habitats and displays a weedy population dynamic with high colonization and extinction rates. The motivation for the study was to understand what factors may be influencing genetic connectedness among newly colonized populations within a regional metapopulation. By using experimental populations composed of genotypes homozygous at a diagnostic locus, it was possible to identify explicitly pollen movement into a focal patch as a function of flower number and distance to the nearest neighboring patch. Overall, the mean immigration rate (measured as the fraction of seeds sired by males outside the focal patch) at 20 m was just over 47%, whereas at 80 m immigration rates were less than 6%. In addition, by knowing the context in which each of these gene-flow events occurred, it was possible to understand some of the factors that influenced the exchange of genes. Both the number of flowers in the focal population (target) and in the neighboring populations (source) had a significant effect on the frequency of gene flow. Our experimental data also demonstrate that factors that influence gene flow at one spatial scale may not act in the same way at another. Specifically, the influence of target size and the relative size of the target and source patches on rates of gene flow depended on whether the patches were separated by 20 m or 80 m. These data suggest that the patterns of gene flow within a metapopulation system can be complex and may vary within a growing season.

Richards, C. M., S. N. Emery, et al. (2003). "Genetic and demographic dynamics of small populations of *Silene latifolia*." *Heredity* 90(2): 181-186.

Small local populations of *Silene alba*, a short-lived herbaceous plant, were sampled in 1994 and again in 1999. Sampling included estimates of population size and genetic diversity, as measured at six polymorphic allozyme loci. When averaged across populations, there was very little change between samples (about three generations) in population size, measures of within-population genetic diversity such as number of alleles or expected heterozygosity, or in the apportionment of genetic diversity within and among populations as measured by F-st. However, individual populations changed considerably, both in terms of numbers of individuals and genetic composition. Some populations doubled in size between samples, while others shrank by more than 75%. Similarly, expected heterozygosity and allele number increased by more than two-fold in individual populations and decreased by more than threefold in others. When population-specific change in number and change in measures of genetic diversity were considered together, significant positive correlations were found between the demographic and genetic variables. It is speculated that some populations were released from the demographic consequences of inbreeding depression by gene flow.

Roche, B. M., H. M. Alexander, et al. (1995). "Dispersal and disease gradients of anther-smut infection of *Silene alba* at different life stages." *Ecology* 76: 1863-1871.

TW; parasitism; host pathogen interaction; *Silene*; spores; dispersal; *Ustilago*; Caryophyllaceae; Ustilaginales; androecium; interaction

Given the increased recognition of the importance of spatial aggregation of infected individuals on disease spread, we used a held experiment to examine spore dispersal and disease transmission at increasing distances from an inoculum source in a well-studied system, the herbaceous plant *Silene alba*, infected by the anther-smut fungus *Ustilago violacea*. Two different life stages (vegetative and floral) were examined. We measured spore deposition on flowers and, as an analog of dispersal to vegetative plants, in small vials on the ground. Spore and disease gradients (number of spores or proportion of plants infected as a function of distance) were best fit with the classic power law, $Y = aD^{-b}$. The slope parameter, b , was similar for spore dispersal gradients of vegetative ($b = -2.38$) and flowering plants ($b = -1.91$). However, at every distance measured, the proportion of flowers with spores was higher than the proportion of ground vials with spores, indicating overall higher relative spore dispersal to flowering plants. We also determined that disease gradients for flowering plants were more shallow ($b = -0.07$) than spore dispersal gradients, and vegetative infection was more spatially restricted than floral infection (no infection beyond 3.2 m for vegetative plants while floral infection was detected up to 11.2 m). The relationship between spore dispersal and disease incidence was linear for vegetative plants and curvilinear for flowering plants, with limiting returns on disease after a low threshold number of spores deposited. Overall, our study suggests that the

limited dispersal of spores is likely to be important in the aggregation of diseased plants in nature; such aggregation of inoculum in turn can increase or decrease disease spread depending on how much inoculum is needed to cause infection.

Rohweder, O. (1967). "Centrospermen-Studien. 3. Blütenentwicklung und Blütenbau bei Silenoideen (Caryophyllaceae)." *Botanische Jahrbücher* 86(1-4): 130-185.
TW; *Silene*; Caryophyllaceae; *Dianthus*; flower; morphology; ontogeny; development

Runyeon, H. and P. H. C. (1996). "Genetic structure in the species-pair *Silene vulgaris* and *S. uniflora* (Caryophyllaceae) on the Baltic island of Oland." *Ecography* 19(2): 181-193.
genetics; *Silene*; Caryophyllaceae; allozyme; demography; Scandinavia; Europe; population; gene flow

Allozyme data were used to assess the genetic structure between 37 sympatric populations of the species-pair *Silene vulgaris* and *S. uniflora* ssp. *petraea*, and to infer levels of intra- and interspecific gene flow in the two species. *Silene vulgaris* is a geographically widespread weed of disturbed habitats whereas *S. uniflora* ssp. *petraea* is endemic to the Baltic islands of Oland and Gotland. On Oland, *Silene vulgaris* forms extensive linear populations along roads while *S. uniflora* ssp. *petraea* occurs in sparse and spatially-separated populations in open limestone habitats. Despite the differences in population size and structure between the two species, both species show extremely low levels of between-population differentiation. Between-site differences account for 2% of the total allozyme diversity within Oland in *S. vulgaris*, and 1% in *S. uniflora* ssp. *petraea*. Indirect estimates of gene flow are high for both species ($Nm = 11$ and 27 , respectively). There is no relationship between genetic distance and geographic distance within either species, and the lack of genetic structure is consistent with the pollination biology of the species - both of which are predominantly moth-pollinated. The two species hybridize in intermediate habitats, and the geographic distribution of species-characteristic alleles indicates a potential for spatially extensive interspecific gene flow. Nevertheless, there are significant differences in allele frequencies between the two species and multivariate analyses show no overlap between populations of the two species. The species are ecologically separated by their different habitat preferences and by differences in their flowering phenology. There is no evidence that the endemic *S. uniflora* ssp. *petraea* is threatened by genetic contamination or assimilation by the widespread weed, *S. vulgaris*.

Runyeon, H. and H. C. Prentice (1997). "Patterns of seed polymorphism and allozyme variation in the bladder campions, *Silene vulgaris* and *Silene uniflora* (Caryophyllaceae)." *Canadian Journal of Botany* 75(11): 1868-1886.
TW; allozyme; biogeography; seed ;shape; *Silene*; Caryophyllaceae; demography; electrophoresis; morphology; testa

Seed morphology (testa ornamentation and seed shape) and allozyme variation were investigated in three closely related and partially sympatric taxa of *Silene* in the Nordic region. Within this region, *Silene vulgaris* is a widespread weed of anthropogenic habitats. The two subspecies of *Silene uniflora* are restricted to naturally open habitats; ssp. *uniflora* has a coastal distribution, whereas the Swedish endemic, ssp. *Petraea*, is restricted to limestone habitats on the islands of Oland and Gotland. All three taxa show a seed ornamentation polymorphism, with individuals producing either tubercled or smooth ("armadillo") seeds. Both seed morphology and allozymes show a separation between the two species *Silene vulgaris* and *Silene uniflora* and support the present taxonomic treatment of the endemic "petraea" as a subspecies of *Silene uniflora*. Tubercled seeds predominate in *Silene vulgaris* and armadillo seeds predominate in *Silene uniflora*. However, there is considerable between-population variation in seed morph frequencies within taxa. In contrast to the other two taxa, populations of *Silene uniflora* ssp. *Petraea* consistently show intermediate frequencies of both seed morphs. *Silene uniflora* ssp. *Petraea* has the lowest between-population component of diversity in both seed shape (18-46%) and allozymes (0.8%) and shows no significant geographic structure in any of the character sets. Both *Silene uniflora* ssp. *Uniflora* and *Silene vulgaris* show significant geographic differentiation in allozymes and seed morphology. The highest between-population component of diversity was found in *Silene uniflora* ssp. *Uniflora*, where 17% of the total allozyme diversity and 39-82% of the seed shape diversity are accounted for by differences between populations.

Sandbrink, J. M., L. J. N. Geurts, et al. (1989). "Chloroplast DNA variation in *Silene* section *Elisanthe* demonstrates *Silene noctiflora* L. is not properly classified." *Biochemical Systematics and Ecology* 17: 539-549.
taxonomy; systematics; DNA; genetics; *Silene*; Caryophyllaceae; molecular biology; evolution; TW

- Schmied, M. (2000). Wechselbeziehungen zwischen *Silene*-Arten und nachtaktiven Faltern. Department of systematic Botany and Ecology. Ulm, University of Ulm.
TW; *Silene*; Caryophyllaceae; Noctuidae; Sphingidae; Germany; Europe; interaction; pollination; nectar; oviposition; mutualism; parasitism; Lepidoptera; nocturnal; reproduction;
- Schulz, A. (1905). "Das Blühen der einheimischen Arten der Gattung *Melandrium*." Beihefte zum Botanischen Centralblatt 17: 287-318.
TW; phenology; flower; *Silene*; Caryophyllaceae; Europe;
- Searcy, K. B. and D. L. Mulcahy (1985). "Pollen tube competition and selection for metal tolerance in *Silene dioica* (Caryophyllaceae) and *Mimulus guttatus* (Scrophulariaceae)." *American Journal of Botany* 72: 1695-1699.
TW; *Mimulus*; ions; metal; Scrophulariaceae; *Silene*; pollen tube growth; competition; EM; Caryophyllaceae; pollen;
- Searcy, K. B. and D. L. Mulcahy (1985). "The parallel expression of metal tolerance in pollen and sporophytes of *Silene dioica* (L.) Clairv., *S. alba* (Mill.) Krause and *Mimulus guttatus* DC." *Theoretical and Applied Genetics* 69: 597-602.
TW; *Mimulus*; ions; Scrophulariaceae; metal; pollen; *Silene*; EM; Caryophyllaceae
- Searcy, K. B. and D. L. Mulcahy (1985). "Pollen selection and the gametophytic expression of metal tolerance in *Silene dioica* (Caryophyllaceae) and *Mimulus guttatus* (Scrophulariaceae)." *American Journal of Botany* 72: 1700-1706.
TW; pollen; pollination; metal; *Silene*; Caryophyllaceae; Scrophulariaceae; pollen stigma interaction; pollen tube growth; selection
- Shehata, A. and M. Zenkteler (1991). "In vitro placental self and cross pollination in some species." *Acta Societatis Botanicorum Poloniae* 60(1-2): 93-99.
in vitro; breeding system; pollination; artificial pollination; autogamy; xenogamy
Excised Placentae with ovules of *Primula pubescens*, *P. auricula*, *Scopolia carniolica*, *Digitalis purpurea*, *Torenia fournieri* and *Chionodoxa luciliae* were self pollinated in vitro and the development of seeds was observed. The same method was used for obtaining hybrid globular embryos from crosses between: *P. pubescens* times *P. auricula*, *Scopolia carniolica* times *Physochlaina praealta*, *Melandrium album* times *Silene saxifraga* and *M. album* times *Arenaria pungens*.
- Shoup, J. R., J. Overton, et al. (1981). "Ultrastructure and development of the nexine and intine in the pollen wall of *Silene alba* (Caryophyllaceae)." *American Journal of Botany* 68(4): 1090-1095.
TW; Caryophyllaceae; electronmicroscopy; *Silene*; pollen; morphology; lightmicroscopy; REM;
- Shykoff, J. and C. Galen (1987). "Differential pollination efficiency of sex morphs of *Silene acaulis* L. Is sexual selection maintaining females?" *American Journal of Botany* 74(5): 658.
pollination; efficiency; *Silene*; Caryophyllaceae; dimorphism; sex; selection; sexual systems; breeding system
- Shykoff, J. A. (1988). "Maintenance of gynodioecy in *Silene acaulis* (Caryophyllaceae), stage-specific fecundity and viability selection." *American Journal of Botany* 75: 844-850.
TW; breeding system; gynodioecy; *Silene*; Caryophyllaceae; seed; Reproduction; germination; sex; pollination; sexual systems
- Shykoff, J. A. (1992). "Sex polymorphism in *Silene acaulis* (Caryophyllaceae) and the possible role of sexual selection in maintaining females." *American Journal of Botany* 79: 138-143.
tw; Caryophyllaceae; dimorphism; sexual systems; selection; sex; *Silene*; Polymorphism; EM; artificial pollination; gynodioecy
- Shykoff, J. A. (1997). "Sex differences in floral nectar production by *Silene latifolia* (Caryophyllaceae), with reference to susceptibility to a pollinator-borne fungal disease." *Canadian Journal of Botany* 75(9): 1407-1414.
TW; Ustilaginales; Mycophyta; pollination; Caryophyllaceae; *Silene*; Nectar; Interaction; demography; sex; dimorphism; parasitism; sugar
Nectar production and concentration were measured on male and female plants of six experimental lines of *Silene latifolia* (Caryophyllaceae) that differ in disease resistance. Differences between the

sexes and among the lines were found for nectar production, concentration, and total sugar production during the first 24 h of anthesis. Females produced more nectar of lower concentration than did males, and males secreted more sugar than did females during the first day of anthesis. However, nectar traits of males and females resembled one another within a line, suggesting a genetic correlation between the sexes. Further, the additive genetic basis for this trait appears weak. In *S. latifolia* repeatabilities for nectar traits were low and differed between females and males, so the heritabilities must be extremely low. Groups of plant lines that are "susceptible" and "resistant" to the fungal pathogen *Microbotryum violaceum* did not differ in nectar parameters. Therefore resistance to this pollinator-borne disease does not appear to influence nectar production.

Shykoff, J. A. and E. Bucheli (1995). "Pollinator visitation patterns, floral rewards and the probability of transmission of *Microbotryum violaceum*, a venereal disease of plants." *J. Ecol.* 83: 189-198.
TW; pollination; pollinator behavior; flower; Mycophyta; Ustilaginales; Nectar; *Silene*; Caryophyllaceae; floral traits; foraging theory; Parasitism

Shykoff, J. A. and O. Kaltz (1997). "Effects of the anther smut fungus *Microbotryum violaceum* on host life-history patterns in *Silene latifolia* (Caryophyllaceae)." *International Journal of Plant Sciences* 158(2): 164-171.

TW; EM; Reproduction; Interaction; demography; Caryophyllaceae; *Silene*; Ustilaginales; parasitism; host pathogen interaction

This study investigated the role of genetic variation among host plants and fungal pathogen on disease prevalence and pathogen-induced phenotypic changes. Four different maternal sibships of *Silene latifolia* showed no difference in susceptibility to disease by the anther smut fungus *Microbotryum violaceum* after inoculation of an infectious mixture containing haploid sporidia of both mating types into the growing rosette. Three different combinations of sporidia were used. Two selfing combinations, one using fungus collected from the same population as the host plants, one from a second population, and one cross between strains from the two populations were generated. The three sporidia combinations did not differ in their success in infecting the host plant and sporulating in the flowers. However, this fungal disease altered host plant phenotype in several important ways. Disease retarded flowering in those male plants that initiated flowering in their first season, and it increased the number of flowers produced by both male and female plants. Different fungal strains differentially augmented flower production, indicating that there is genetic variability for important fitness-related life-history traits in natural populations of the fungus *M. violaceum* in Europe. Furthermore, in this short-lived perennial host plant, diseased plants were more likely than were healthy ones to initiate flowering in their first growing season. Since this shift from vegetative growth to reproduction should enhance fungal reproductive success, we interpret this as a manipulation of the host plant phenotype by the fungus. In addition we found a significantly female-biased sex ratio across the four maternal sibships in this study and higher infection rates for female plants than males.

Shykoff, J. A. and O. Kaltz (1998). "Phenotypic changes in host plants diseased by *Microbotryum violaceum*: Parasite manipulation, side effects, and trade-offs." *International Journal of Plant Sciences* 159(2): 236-243.

infection; *Silene*; Ustilaginales; gender dimorphism; floral traits; phenotype; interaction; Caryophyllaceae; pathogen; Mycophyta; parasitism

Parasites induce changes in their hosts that can be viewed either as pathological effects of infection (i.e., symptoms), adaptive defense by the host, or adaptive manipulation on the part of the parasite. The pollinator-borne anther-smut fungus *Microbotryum violaceum* is a prevalent parasite of the common roadside weed *Silene latifolia* (Caryophyllaceae). The fungal disease alters the phenotype of the host plant in several important ways. In a greenhouse experiment, we show that the disease accelerated flowering and that diseased plants invested relatively less in root biomass than did healthy plants. In a second experiment, diseased plants also produced smaller, more irregularly shaped flowers with different nectar-sugar production than did healthy plants. The magnitude of some of these effects of the disease differed for different fungal crosses. Differential alteration of host phenotype may result in pollinator-mediated selection on this pathogen. Whereas some of these changes in host phenotype may represent parasite adaptations, others may represent side effects of disease. It also appears that although the parasite modifies host phenotypes, trade-offs become evident, such as those between flower size and flower number and investment to vegetative compared with storage biomass. This indicates that this fungus cannot produce a plant phenotype optimal for pollinator attraction and disease transmission.

Siikamaki, P. and A. Lammi (1998). "Fluctuating asymmetry in central and marginal populations of *Lychnis viscaria* in relation to genetic and environmental factors." *Evolution* 52(5): 1285-1292.

Developmental instability in the form of increased fluctuating asymmetry can be caused by either genetic or environmental stress. Because extinctions can be attributed broadly to these factors, fluctuating asymmetry may provide a sensitive tool for detecting such stresses. We studied the level of fluctuating asymmetry of flowers of a perennial outcrossing plant species, *Lychnis viscaria*, both in natural and common-garden populations. The degree of flower asymmetry was higher in small, isolated, and marginal populations of the species range. These marginal populations also were the most homozygous. In the core area of the species' range, flowers were more symmetrical. The level of asymmetry was correlated with both population size and heterozygosity. However, a partial correlation analysis revealed that when the impact of population size was controlled for, there was a negative relationship between fluctuating asymmetry and heterozygosity, whereas when controlling for heterozygosity, no relationship between population size and fluctuating asymmetry was found. This indicates that genetic consequences of small population size probably underlie the relationship between the level of asymmetry and population size. Results from a transplantation experiment showed that individuals subjected to a higher environmental stress had an increased level of asymmetry compared to control plants. In the common-garden conditions the level of fluctuating asymmetry did not differ between the central and marginal populations. This suggests that presumably both genetic and environmental factors affected to the higher level of asymmetry among marginal populations compared to central ones. In all, we conclude that even though fluctuating asymmetry seems to be a sensitive tool for detecting stresses, results from studies focusing on only one factor should be interpreted with caution.

Siikamaki, P., A. Lammi, et al. (2002). "No relationship between fluctuating asymmetry and fitness in *Lychnis viscaria*." *Evolutionary Ecology* 16(6): 567-577.

TW; fitness; *Lychnis*; *Silene*; Caryophyllaceae; symmetry; flower; morphology; Petalum; seed; biomass; evolution

Several earlier studies have indicated a negative relationship between fluctuating asymmetry (FA) and fitness. We tested this assumption by investigating the association between petal asymmetry and several fitness-related characters among natural and common garden populations of *Lychnis viscaria*. Neither seed set, germination percentage nor the growth rate of seedlings were related to the level of flower asymmetry either among natural populations or in common garden conditions. The only significant association found was a positive connection between petal asymmetry and seed mass measured from natural populations. Thus, in contrary to many earlier published reports, we did not find any evidence for a negative relationship between FA and fitness even if we controlled for measurement error, we had adequate sample size and we measured these characters in two environments. This suggests that FA is not consistently related to individual quality and fitness.

Siikamaki, P., A. Lammi, et al. (1996). "Reproductive success of the sticky catchfly (*Lychnis viscaria*) in relation to population size and isolation." *Bulletin of the Ecological Society of America* 77(3 Suppl., Part 2): 407.

Lychnis; Caryophyllaceae; reproduction; success; population; size; isolation

Simmons, E. G. (2002). "Alternaria themes and variations (287-304) - Species on Caryophyllaceae." *Mycotaxon* 82: 1-40.

Dianthus; Gypsophila; *Saponaria*; *Silene*; Stemphylium; *Vaccaria*

A continuation of a series of papers primarily on *Alternaria*, in this instance for phaeodictyosporic taxa described from hosts/substrates in the Caryophyllaceae. Of the 24 names published validly or invalidly for this group (1876 to date), 12 are retained for identifiable taxa in *Alternaria* and *Stemphylium*. of these 12 names, seven are presented in novel formats, including *A. nobilis* (syn. *A. dianthi*; on *Dianthus caryophyllus*), *S. bubakii* (on *Silene nutans*), *A. vaccariae* (on *Vaccaria pyramidalis*), *S. trisectum* (on *Silene inflata*), *A. ellipsoidea* (on *Dianthus barbatus*), *A. juxtiseptata* (on *Gypsophila paniculata*), and *A. subelliptica* (on *G. paniculata*). A diagnostic key to the nine species retained in *Alternaria* is provided.

Skogsmyr, I. (1993). "Male reproductive investment and venereal diseases in plants: The case of the sticky catchfly, *Lychnis viscaria*." *Oikos* 66(2): 209-215.

TW; male and female function; costs; reproduction; Caryophyllaceae; *Lychnis*; host pathogen interaction; parasitism; interaction; inflorescence; size; pollinator attraction;

The fungus *Ustilago violacea* is dispersed between certain caryophyllaceous plants, including *Lychnis viscaria*, by pollinating insects. Infection leads to sterility the following season when the infected plant produces fungal spores instead of pollens. Attraction of pollinators is thus associated

not only with the cost of producing flowers but also with a risk of becoming infected by the fungus. In this paper I analyse male lifetime reproductive success as a function of incidence of infection in a population, cost of flower production and attractiveness to pollinators (measured as size of the inflorescence). Both lifetime reproductive success and optimal number of flowers are predicted to relate negatively to the incidence of infection in a population. This is a result of shortened reproductive lifetime due to infection and a lower fertilization, as some pollen will be deposited on infected recipients. Lifetime reproductive success is further affected by the cost of producing flowers and the number of ovules in the recipient. Changing reproductive strategies in the population as a result of different incidences of infection, may in turn affect ovule number.

Soldaat, L. L., B. Vetter, et al. (1997). "Sex ratio in populations of *Silene otites* in relation to vegetation cover, population size and fungal infection." *Journal of Vegetation Science* 8(5): 697-702.

TW; habitat; population; *Ustilago*; infection; dioecy; Caryophyllaceae; demography; EM; sex; sex ratio; sexual systems; *Silene*; vegetation; demography; phenology; breeding system; Mycophyta; Ustilaginales; Parasitism; host pathogen interaction

In contrast to populations of most dioecious *Silene* species (which usually are female-biased), populations of *Silene otites* have been frequently reported to be male-biased. We describe sex ratio variation in 34 natural *S. Otites* populations in Central Germany in relation to vegetation cover, population size and fungal infection. The overall sex ratio was unbiased in 1994 and only slightly male-biased in 1995. Sex ratio Varied among the populations from 26.6 % to 72.6 % females. The sex ratio of small populations varied strongly due to stochastic processes. Furthermore, we found that populations in habitats with high vegetation cover contained a higher percentage of females. Hermaphroditic plants, theoretically, could increase male bias as they only produce male or hermaphroditic offspring. Their frequency in the populations, however, was far too low to affect sex ratio. In 1994 12.1 % and in 1995 17.0 % of the plants were infected by the smut fungus *Ustilago major*. Disease incidence in the population was not related to sex ratio, suggesting equal susceptibility of males and females. The sex ratio of partially infected plants did not deviate from the population sex ratio, both under field conditions and in a greenhouse laboratory experiment. The results suggest that the frequently reported male bias in *Silene otites* populations is not a general pattern, but is mainly caused by environmental conditions.

Sourková, M. (1971). "Pleconax Rafin. - eine bis heute unbeachtete Silenoideen-Gattung (Caryophyllaceae)." *Österreichische Botanische Zeitschrift* 119: 577-581.

TW; Caryophyllaceae; *Silene*; taxonomy; systematics

Stadler, T. and L. F. Delph (2002). "Ancient mitochondrial haplotypes and evidence for intragenic recombination in a gynodioecious plant." *Proceedings of the National Academy of Sciences of the United States of America* 99(18): 11730-11735.

gene; mitochondrion; mutation; variation; gynodioecy; *Silene*; alpine; Caryophyllaceae; mtDNA; breeding system; evolution

Because of their extremely low nucleotide mutation rates, plant mitochondrial genes are generally not expected to show variation within species. Remarkably, we found nine distinct cytochrome b sequence haplotypes in the gynodioecious alpine plant *Silene acaulis*, with two or more haplotypes coexisting locally in each of three sampled regions. Moreover, there is evidence for intragenic recombination in the history of the haplotype sample, implying at least transient heteroplasmy of mitochondrial DNA (mtDNA). Heteroplasmy might be achieved by one of two potential mechanisms, either continuous coexistence of subgenomic fragments in low stoichiometry, or occasional paternal leakage of mtDNA. On the basis of levels of synonymous nucleotide substitutions, the average divergence time between haplotypes is estimated to be at least 15 million years. Ancient coalescence of extant haplotypes is further indicated by the paucity of fixed differences in haplotypes obtained from related species, a pattern expected under trans-specific evolution. Our data are consistent With models of frequency- dependent selection on linked cytoplasmic male-sterility factors, the putative molecular basis of females in gynodioecious populations. However, associations between marker loci and the inferred male-sterility genes can be maintained only with very low rates of recombination. Heteroplasmy and recombination between divergent haplotypes imply unexplored consequences for the evolutionary dynamics of gynodioecy, a widespread plant breeding system.

Städler, T. and L. F. Delph (2002). "Ancient mitochondrial haplotypes and evidence for intragenic recombination in a gynodioecious plant." *Proceedings of the National Academy of Sciences of the United States of America* 99(18): 11730-11735.

TW; mitochondrium; genetics; molecular biology; phylogeny; gynodioecy; sex; cytochrome; *Silene*; Caryophyllaceae; male sterility; alpine; breeding system

Because of their extremely low nucleotide mutation rates, plant mitochondrial genes are generally not expected to show variation within species. Remarkably, we found nine distinct cytochrome b sequence haplotypes in the gynodioecious alpine plant *Silene acaulis*, with two or more haplotypes coexisting locally in each of three sampled regions. Moreover, there is evidence for intragenic recombination in the history of the haplotype sample, implying at least transient heteroplasmy of mitochondrial DNA (mtDNA). Heteroplasmy might be achieved by one of two potential mechanisms, either continuous coexistence of subgenomic fragments in low stoichiometry, or occasional paternal leakage of mtDNA. On the basis of levels of synonymous nucleotide substitutions, the average divergence time between haplotypes is estimated to be at least 15 million years. Ancient coalescence of extant haplotypes is further indicated by the paucity of fixed differences in haplotypes obtained from related species, a pattern expected under trans-specific evolution. Our data are consistent with models of frequency-dependent selection on linked cytoplasmic male-sterility factors, the putative molecular basis of females in gynodioecious populations. However, associations between marker loci and the inferred male-sterility genes can be maintained only with very low rates of recombination. Heteroplasmy and recombination between divergent haplotypes imply unexplored consequences for the evolutionary dynamics of gynodioecy, a widespread plant breeding system.

Talavera, S., M. Arista, et al. (1996). "Population size, pollination and breeding system of *Silene stockenii* Chater (Caryophyllaceae), an annual gynodioecious species of Southern Spain." *Botanica Acta* 109: 333-339.

TW; Caryophyllaceae; *Silene*; pollination; reproduction; demography; Spain; Europe; gynodioecy; EM;

Taylor, D. R. (1994). "Sex ratio in hybrids between *Silene alba* and *Silene dioica*: evidence for Y-linked restorers." *Heredity* 73: 518-526.

TW; sex; hybrid; *Silene*; Caryophyllaceae; genetics;

Taylor, D. R. (1996). "Parental expenditure and offspring sex ratios in the dioecious plant *Silene alba* (= *Silene latifolia*)." *American Naturalist* 147: 870.

TW; Caryophyllaceae; gender dimorphism; *Silene*; dioecy; sex; sex ratio; breeding system; competition; reproduction; evolution; sexual system

Taylor, D. R. (1999). "Genetics of sex ratio variation among natural populations of a dioecious plant." *Evolution* 53(1): 55-62.

TW; genetics; sex; dioecy; *Silene*; Caryophyllaceae; demography; sexual system; sex ratio
The female-biased sex ratio in the genus *Silene* is the most widely documented example of sex ratio bias in plants. It has recently been shown that the genetic basis of sex ratio in this species involves a system of sex ratio distorters and restorers, but it is not known if these genetic elements are of fundamental importance in natural populations. I crossed plants from natural populations with known testers to examine the frequencies of sex ratio distorters and restorers in eight populations of *S. alba*, and to determine the extent that these elements are responsible for the sex ratio variation in nature. The genetic basis of sex ratio varied from one population to another, suggesting that sex ratio evolution occurs over a relatively small spatial scale and is asynchronous among local demes. The resulting variation in the frequency of sex ratio alleles among populations explained most of the sex ratio variation seen in nature, which suggests that the ecology and evolution of this trait in natural populations is governed primarily by underlying dynamics of selfish genetic elements. The possible causes and the evolutionary consequences of population structure at genes controlling sex ratio are discussed, as are the implications of these results for the overall importance of selfish genetic elements in natural populations.

Taylor, D. R. and P. K. Ingvarsson (2003). "Common features of segregation distortion in plants and animals." *Genetica* 117(1): 27-35.

evolution; theory; gene; heritability; genetics; chromosomes

Segregation distortion is increasingly recognized as a potentially powerful evolutionary force. This runs counter to the perception that non-Mendelian genes are rare genetic curiosities, a view that seems to be supported by the near ubiquity of the Mendelian system of inheritance. There are several reasons why segregation distortion may be more important than is evidenced by known empirical examples. One possibility is that the types of segregation distorters we have found are only a subset of a broader range of non-Mendelian systems, many of which go undetected. In this

paper, we review what is known about the sex-linked meiotic drive system in the plant, *Silene latifolia*, and present some data on the mechanism of segregation distortion. We outline the general features that segregation distorters in plants and animals have in common. In some cases, such as the paucity of systems that directly alter meiotic segregation, there are likely to be inherent constraints on the range of systems that can possibly occur. Other generalities, however, support the notion that many forms of meiotic drive are possible, and that the known examples of segregation distortion are likely to be only subset of those that can possibly occur. Non-Mendelian genes may therefore have greater evolutionary importance than their current abundance in nature would suggest.

- Thomas, A., J. Shykoff, et al. (2003). "Sex-ratio bias in populations of the phytopathogenic fungus *Microbotryum violaceum* from several host species." *International Journal of Plant Sciences* 164(4): 641-647.
Ustilaginales; pathogen; parasitism; Mycophyta; spores; sex ratio; genetics; heritability
The present study explores the maintenance of a segregation distortion in the phytopathogenic fungus *Microbotryum violaceum* (anther smut). Some individuals of this species produce spores with completely biased sex ratio because of the presence of haplo-lethal alleles linked to the mating-type gene. To test the different hypotheses proposed to explain the maintenance of these haplo-lethal alleles (diploid advantage to counterbalance haploid deleterious effects, neutrality of haplo-lethal alleles only in populations with high interstrain competition, and complete neutrality), sex-ratio bias was investigated in natural European populations of *M. violaceum* from *Silene latifolia* and other species of Caryophyllaceae. The negative relationship observed between proportions of strains expressing a sex-ratio bias and disease prevalence was opposite the one predicted by the second hypothesis. On the contrary, the pattern of the variances, with proportions of biased strains more extreme in smaller populations, fitted perfectly with the prediction of the third hypothesis. Experimental studies are now needed to confirm the complete neutrality of the haplo-lethal alleles linked to the mating-type gene in *M. violaceum*.
- Thompson, P. A. (1970). "Germination of species of Caryophyllaceae in relation to their geographical distribution in Europe." *Annals of Botany* 84: 427-449.
TW; germination; *Silene*; Caryophyllaceae; distribution; seed; Europe; reproduction; EM
- Thompson, P. A. (1981). "Variations in seed size within populations of *Silene dioica* (L.) Clairv. in relation to habitat." *Annals of Botany* 47: 623-634.
TW; seed; demography; seed set; reproduction; *Silene*; Caryophyllaceae; biomass; habitat
- Thrall, P. H., A. Biere, et al. (1993). "Plant life-history and disease susceptibility- the occurrence of *Ustilago violacea* on different species within the Caryophyllaceae." *Journal of Ecology* 81: 489-498.
TW; Ustilaginales; Mycophyta; Caryophyllaceae; *Silene*; reproduction; coevolution; *Ustilago*; parasitism; EM; host pathogen interaction
- Van Nigtevecht, G. and J. Van Brederode (1975). "Flavonoid glycosylation genes in European populations of *Silene dioica* and *Silene alba*." *Heredity* 35(3): 429.
Silene; Caryophyllaceae; flavonoids; gene; population
- Van Rossum, F., J. De Bilde, et al. (1996). "Barriers to hybridization in calcicolous and silicicolous populations of *Silene nutans* from Belgium." *Belgian Journal of Botany* 129(1): 13-18.
TW; *Silene*; hybrid; Belgium; Stigma; pollen; isolation; population; allozyme; sympatric;
In Belgium, *Silene nutans* has evolved very distinct populations in relation to the nature of the bedrock, calcareous or siliceous: striking divergences occur in flower, infructescence, fruit, and seeds features as well as in allozyme markers. This paper shows that barriers to crossing were strong between the two types of populations both at the prezygotic (pollen-stigma incompatibility) and postzygotic (F1 hybrids sterility) stages. Calcicolous (Ca-) and silicicolous (Si-) populations from Belgium have reached an advanced stage in the sympatric differentiation process. Such a level of differentiation is not found in other parts of Europe.
- Van Rossum, F., X. Vekemans, et al. (1997). "Allozyme variation in relation to ecotypic differentiation and population size in marginal populations of *Silene nutans*." *Heredity* 78: 552-560.
TW; allozyme; demography; ecology; *Silene*; Caryophyllaceae; genetics; Europe;
- Veuskens, J., D. Marie, et al. (1995). "Flow sorting of the Y sex chromosome in the dioecious plant *Melandrium album*." *Cytometry* 21: 363-373.

TW; *Silene*; gene; sexual system; flow cytometry; sex; Caryophyllaceae; genetics; dioecy; methods; chromosomes;

The preparation of stable chromosome suspensions and now cytometric sorting of both the Y sex chromosome of the white campion, *Melandrium album*, and the deleted Y chromosome of an asexual mutant, 5K63, is described. The principle has been to maintain transformed roots in vitro, synchronise and block mitosis, reduce cells to protoplasts, and lyse these to release chromosomes. Such in vitro material, unlike many cell suspensions, showed a stable karyotype. Factors critical to producing high-quality chromosome suspensions from protoplasts include osmolality of isolation solutions and choice of spindle toxin and of lysis buffer. *Agrobacterium rhizogenes* transformed young growing root cultures were synchronised at G1/S with 50 μ M aphidicolin for 24 h and released to a mitotic block with 30 μ M oryzalin for 11 h. Protoplast preparations from such tissue routinely had metaphase indices reaching 15%. Suspensions of intact metaphase chromosomes, with few chromatids, were obtained by lysing swollen mitotic protoplasts in a citric acid/disodium phosphate buffer. Except for the presence of clumps of autosomal chromosomes near the X and Y chromosome zones, monoparametric histograms of fluorescence intensities of suspensions stained with 4',6-diamidino-2-phenylindole showed profiles similar to theoretical now karyotypes. Two types of Y chromosomes, one full-length and one partially deleted (from the asexual mutant), could be sorted at 90% purity (21-fold enrichment of Y). These results are discussed in the context of sex determination and differentiation in higher plants. (C) 1995 Wiley-Liss, Inc.

Vogel, S. (1998). "Remarkable nectaries: Structure, ecology, organophyletic perspectives III. Nectar ducts." *Flora* 193(2): 113-131.

TW; nectar; nectaries; Alliaceae; Violaceae; Wachendorfia; *Silene*; Capsicum; Haemodoraceae; Caryophyllaceae; Scrophulariaceae; Solanaceae; Linaria; spur; anatomy; morphology

The present, third part of a series of studies on floral and extrafloral nectaries deals with auxiliary structures whose function is to conduct nectar from its source towards a more or less distant site of exposition. Ducts occur especially in plant groups that have a fixed conformation of floral organs and have been unable to dislocate the nectary towards a site more appropriate for pollination, such as spurs and narrow tubular containers. These drainage systems are concealed, preventing access to visitors. In all known cases, they run externally in capillary clefts between floral organs or in tubes 20-70 μ m in diam., formed by invaginations of the cutinized but easily wettable epidermal surface with +/- tightly connivent margins. The nectar flows along the ducts driven by capillary forces, secretion pressure and, in part, gravity. The Alliaceae, whose papillate septal nectaries principally bear their three primary outlets at the top of the superior ovary, only rarely discharge the fluid directly at these points, a case exemplified by *Allium cernuum*. In Brodiaea and Nothoscordum, cryptic ducts run along the external carpellary sutures towards the base of the ovary, where the nectar is released. In *Triteleia* and *Dichelostemma*, they continue proximally along an ovarial stipe that extends the distance between the source and the site of nectar deposition. An extreme is achieved in *Milla*, whose stipe is connate with the perigon tube by means of three septa; each of the three resulting separate nectar pipes is fed with nectar by ducts which run along the stipe over a distance of up to 13 cm, with apertures in the pipe's lower end. The zygomorphic flowers of *Wachendorfia* (Haemodoraceae), with a semi-inferior, trilocular ovary, have only two nectariferous ovarial septa. These are sunken in the torus and drained by lateral, retroverse channels which conduct the fluid to a pair of external, spur-like auricles of the perigon segments. The nectar of *Silene schafta* and allies (Caryophyllaceae) collects at the bottom of an elongate, tubular calyx. Its source is a disk, borne a considerable distance away - as all remaining floral parts - by a long columnar stipe. The liquid flows within 10 cryptic channels along the stipe and is released at its base above the insertion of the calyx. In *Capsicum* (Solanaceae), nectar produced by an ovarial disk travels through concealed ducts from the inaccessible tubular part of the corolla towards five apertures which lie outside the staminal fascicle on the flat limb. Analogous drainage systems of the related genera *Jaltomata* and *Physalis* are illustrated. The spur of the zygomorphic corollas of *Linaria* and *Kickxia* (Scrophulariac.) is supplied with nectar by means of a single duct which descends from the disk and runs down along the dorsal wall to the spur's tip where the fluid is released into the main lumen of the spur. The Violaceae use different strategies to overcome the problem of supplying long spurs with the nectar they produce by distant connectival glands. In *Corynostylis volubilis* an internal furrow of the spur wall probably assumes this function, leading from the nectar scale to the spur's tip 5 cm away.

Vural, M. and A. A. Donmez (2002). "Two new taxa of *Silene* (Caryophyllaceae) from Turkey." *Annales Botanici Fennici* 39(2): 153-158.

Caryophyllaceae; *Silene*; taxonomy; Turkey

Silene koycegizensis Donmez & Vural sp. nova and *S. cariensis* Boiss. subsp. *muglae* Vural & Donmez subsp. nova (sect. *Behenantha* Othh.) are described from Turkey. Diagnostic characters, description, detailed illustrations and taxonomic comments on the taxa are given. Their relationships with the allied species *S. cretica* L., *S. tenuiflora* Guss. and *S. cariensis* are discussed. Geographic distributions of the new taxa and other related species are shown on maps.

- Waldmann, P. (1999). "The effect of inbreeding and population hybridization on developmental instability in petals and leaves of the rare plant *Silene diclinis* (Caryophyllaceae)." *Heredity* 83: 138-144.
TW; inbreeding; Caryophyllaceae; *Silene*; hybrid; development; flower; leaf
- Weiss, M. R. (1995). "Floral colour change: A widespread functional convergence." *American Journal of Botany* 82: 167-185.
TW; flower; color change; convergent evolution; *Silene*; Caryophyllaceae; pollinator behavior; floral traits; color
- Westerbergh, A. and A. Saura (1992). "The effect of serpentine on the population structure of *Silene dioica* (Caryophyllaceae)." *Evolution* 46: 1537-1548.
TW; *Silene*; Caryophyllaceae; demography; ecology; allozyme; genetics; heavy metal; population
- Westerbergh, A. and A. Saura (1994). "Gene flow and pollinator behaviour in *Silene dioica* populations." *Oikos* 71: 215-224.
TW; *Silene*; Caryophyllaceae; pollination; gene flow; demography; pollinator behavior; EM; Scandinavia
Silene dioica (L.) Clairv. (Caryophyllaceae) is an insect pollinated and obligately cross-fertilising herb commonly found on serpentine, i.e. soils rich in heavy metals, and on cultivated meadows. Groups of *Silene* populations were studied in two areas in the Scandianvian mountains. In a northern area *Silene* populations grow in an open pine and birch forest while in the south, populations are surrounded by a continuous and dense spruce forest. Gene flow, estimated on the basis of allele frequencies, is highly restricted in the south in comparison to the north. This has led to an extensive genetic differentiation among populations. The pollinator guilds (Thricops flies, syrphid flies and bumblebees) are similar in the northern and southern populations and can therefore not account for the difference in gene flow. The flowering in nearby populations overlaps broadly and is also not the reason for the genetic differentiation in the south. The differentiation is more likely due to vegetation that limits pollinator movement. The level of gene flow differs in the two habitats both in the north and in the south. The gene flow is restricted among serpentine populations but common among meadow populations. Pollen dispersal, and in particular, anthropogenic seed dispersal mediate gene flow among meadows. Serpentine populations are unaffected by human activity. Pollinators are therefore the main agent of gene flow on serpentine. This study shows the importance of the surrounding vegetation in influencing gene flow patterns among populations as well as that habitat fragmentation affects the genetic properties of plant populations. In addition, we have also observed a restricted gene flow within populations. Enzyme allele frequencies show an excess of homozygotes within most of the populations. This can be explained through limited pollen dispersal and differences in male and female flowering density.
- Westerbergh, A. and J. Westerbergh (2001). "Interactions between seed predators/pollinators and their host plants: a first step towards mutualism?" *Oikos* 95(2): 324-334.
Silene; Caryophyllaceae; mutualism; pollination; oviposition; Lepidoptera; evolution; behavior; host pathogen interaction; parasitism; predation; model
The mutualisms between fig trees and their pollinator fig wasps and between yucca plants, and yucca moths are spectacular examples of coevolution. The characteristics, of these independently evolved mutualisms have resulted from long-term processes, the first stages of which are unknown. A fundamental question in the study of mutualism is how these interactions evolve. Seed predator/pollinator and host plant interactions, which may initially be considered as mainly antagonistic, have the potential to provide good model systems for the study of the first stages of evolution towards, mutualism. We present here theoretical models assessing the consequences of interactions between specialized seed predator insects and their host plants. These models describe the parameters that affect the fitness of an individual female seed predator and her influence on the fitness of the host plant. In an optimal strategy for the seed predator, the number of eggs laid in each flower depends on the interaction between the adult and larva survival. Along with a growing predation pressure on adults and larvae several eggs must be laid in each flower by the female seed predator to enhance her fitness. However, in a situation where the host plant selectively aborts flowers with a high number of eggs the fitness of the seed predator will seriously

decrease. If the cost of selective abortion is less than the cost of seed predation the host plant will maintain fitness. In a mutualistic relationship a balance between the cost and the benefit of the parameters in the fitness models of the seed predator and the host plant has to occur so that the net seed output is larger than zero (0). Any unselfish behaviour or quality of the seed predator that would benefit the host plant in such a way that the net seed output increases might be a first stage in an interaction becoming mutualistic. The models presented here will not only provide a platform for empirical studies on interactions that may swing from parasitism to mutualism, but also for seed predator/pollinator and host plant interactions, in general.

- Willis, J. C. and I. H. Burkill (1895). "Flowers and insects in Great Britain. Part I." *Annals of Botany* 9: 227.
TW; *Silene*; Caryophyllaceae; pollination; Great Britain; Europe; melittophily; psychophily; myiophily; entomophily
- Willis, J. C. and I. H. Burkill (1903). "Flowers and insects in Great Britain. Part III. Observations on the most specialized flowers of the Clova Mountains." *Annals of Botany* 17: 539-570.
TW; *Silene*; Caryophyllaceae; pollination; Great Britain; Europe; melittophily; psychophily; myiophily; specialization
- Willis, J. C. and I. H. Burkill (1903). "Flowers and insects in Great Britain. Part II. Observations on the natural orders Dipsacaceae, Plumbaginaceae, Compositae, Umbelliferae, and Cornaceae, made in the Clova Mountains." *Annals of Botany* 17: 313-317.
TW; *Silene*; Caryophyllaceae; pollination; Great Britain; Europe; melittophily; Psychophily; myiophily; Dipsacaceae; Plumbaginaceae; Asteraceae; Apiaceae; Cornaceae
- Wilmanns, O. and S. Rupp (1966). "*Silene rupestris*, das Felsen-Leimkraut, als Glazialrelikt im Schwarzwald." *Mitteilungen des badischen Landesvereins für Naturkunde und Naturschutz* 9: 381-389.
TW; *Silene*; Caryophyllaceae; isolation; endemism; Germany; Europe; distribution; climate;
- Wilson, G. B., J. Wright, et al. (1995). "*Lychnis viscaria* L. (*Viscaria vulgaris* Bernh.)." *Journal of Ecology* 83: 1039-1051.
TW; Caryophyllaceae; Europe; Great Britain; reproduction; pollination; morphology; anatomy; distribution; ecology
- Witt, T. (1994). Reproduktionsbiologie von *Silene*- und *Saponaria*-Arten (Caryophyllaceae) und ihr Blüten- und Nektarangebot. Department of Botany. Giessen, University of Giessen: 141.
TW; nectar; Europe; Germany; melittophily; phalenophily; sphingophily; psychophily; pollination; reproduction; Caryophyllaceae; *Silene*; Noctuidae; Lepidoptera; *Saponaria*; phenology; flowering phenology
- Witt, T. (2003). Reproduktionsbiologie von Caryophyllaceen (Unterfamilie Caryophylloideae) unter besonderer Berücksichtigung der Nektarproduktion. Abteilung Systematische Botanik und Ökologie (Biologie V). Ulm, University of Ulm: 182.
TW; Caryophyllaceae; *Silene*; *Dianthus*; *Lychnis*; *Agrostemma*; *Vaccaria*; nectar; reproduction; seed set; fruit set; experiment; bagging; sugar; amino acid; compounds; secretion; morphology; flower
- Witt, T., A. Jürgens, et al. (1999). "Nectar dynamics and sugar composition in flowers of *Silene* and *Saponaria* species (Caryophyllaceae)." *Plant Biology* 1(3): 334-345.
TW; Caryophyllaceae; *Silene*; *Saponaria*; nectar; secretion; sugar ; phalenophily; sphingophily; melittophily; pollination; rhythm; nocturnal; Caryophylloideae; diurnal
Nectar production in *Saponaria officinalis* and in five species of *Silene* (*S. alba*, *S. dioica*, *S. noctiflora*, *S. nutans*, *S. vulgaris*) was examined during two consecutive years (May to July 1993, and May to June 1994) in the Botanical Garden of the University of Giessen. Nectar volume and sugar concentration were studied in relation to time of day, flower sex, flower age, and flowering stage. Nectar amount in all species studied (except *S. dioica*) increased in the afternoon or in the evening until midnight (or until the early morning in *S. nutans*). After midnight and until midday, nectar volume in non-visited flowers (except *S. dioica*) decreased. Nectar volume in non-visited *S. dioica* flowers increased constantly with flower age, indicating a stable nectar secretion rate, possibly favouring both day- and night-active flower visitors. Even at the time of highest nectar secretion, all species studied presented several nectarless flowers. Sucrose dominance in the nectar of the nocturnal species *S. nutans* and *Saponaria officinalis* fits well with the general syndrome of flowers pollinated by hawkmoths. The syndrome also applies to the nocturnal but

regularly selfing, *S. noctiflora*. The more generalistic species *S. dioica* and *S. vulgaris*, which are regularly visited by bumblebees as well as nocturnal moths, secreted hexose-dominant nectar. Unexpectedly, *Silene alba*, the only nocturnal species that strictly excluded day-active flower visitors by closing flowers during the day, also secreted hexose-dominant nectar. In some cases, nectar volumes and nectar concentration differed significantly between hermaphroditic, male, and female flowers. Female flowers of *S. alba*, *S. dioica*, and *S. nutans* contained significantly less concentrated nectar than male or hermaphroditic (*S. nutans*) ones. In *S. noctiflora* and *S. vulgaris* the difference was not statistically significant but nectar concentration did show the same tendency.

Wolfe, L. M. (2002). "Why alien invaders succeed: Support for the escape-from-enemy hypothesis." *American Naturalist* 160(6): 705-711.

TW; invasion; herbivory; invasion; *Silene*; *Hadena*; Caryophyllaceae; North America; interaction; Ustilaginales; Lepidoptera; Noctuidae

Successful biological invaders often exhibit enhanced performance following introduction to a new region. The traditional explanation for this phenomenon is that natural enemies (e. g., competitors, pathogens, and predators) present in the native range are absent from the introduced range. The purpose of this study was to test the escape-from-enemy hypothesis using the perennial plant *Silene latifolia* as a model system. This European native was introduced to North America in the 1800s and subsequently spread to a large part of the continent. It is now considered a problematic weed of disturbed habitats and agricultural fields in the United States and Canada. Surveys of 86 populations in the United States and Europe revealed greater levels of attack by generalist enemies (aphids, snails, floral herbivores) in Europe compared with North America. Two specialists (seed predator, anther smut fungus) that had dramatic effects on plant fitness in Europe were either absent or in very low frequency in North America. Overall, plants were 17 times more likely to be damaged in Europe than in North America. Thus, *S. latifolia*'s successful North American invasion can, at least in part, be explained by escape from specialist enemies and lower levels of damage following introduction.

Wright, J. W. and T. R. Meagher (2003). "Pollination and seed predation drive flowering phenology in *Silene latifolia* (Caryophyllaceae)." *Ecology* 84(8): 2062-2073.

TW; Caryophyllaceae; phenology; pollination; seed; predation; *Silene*; experiment; resource allocation; fruit set; costs

The development of fruits after pollination places resource demands on plants that may influence the production of subsequent flowers. Pre-dispersal seed-predation, resulting in the destruction of developing seeds, may allow resource reallocation to the production of subsequent flowers. *Silene latifolia*, the white campion, is subject to predispersal seed predation by noctuid moths. In order to determine the potential for resource reallocation in *S. latifolia* we conducted a greenhouse experiment in which female plants were subjected to three levels of pollination (0%, 50%, or 100%) and simulated pre-dispersal seed predation (0%, 50%, or 100% of total fruit production). We assigned 10 plants to each of the seven treatments (0% pollinated had no fruit); in total, 1490 flowers were measured for flower size and scored for date of flowering and longevity. Flower size decreased over the course of the experiment. Average daily production was 12.2 flowers per plant on nonpollinated plants, but only 4.3 flowers on 100% pollinated plants. Chi-square results showed that simulated seed predation resulted in additional flowering bouts later in the course of the experiment. Time series analysis showed that the time between flowering bouts was also influenced by predation. Plants with 0% predation had an average lag time of 29.5 days, whereas plants with 100% simulated seed predation had a lag period of 20.1 days. Flower longevity of non-pollinated flowers increased in plants that had flowers' pollinated but experienced no seed predation.

Simulated predation resulted in a decrease in floral longevity. These results suggest that plants reallocate resources to the production of new flowers, after the destruction of fruits; thus, flowering phenology is influenced by pollination and seed predation. The relationship between pollinators and flowering phenology is well accepted; these results indicate that seed predators play an equally important role in determining flowering phenology.

Wrigley, F. (1986). "Taxonomy and chorology of *Silene* section *otites* (Caryophyllaceae)." *Annales Botanici Fennici* 23: 69-81.

TW; taxonomy; chorology; *Silene*; Caryophyllaceae; Europe

Ye, D., P. Installe, et al. (1990). "Sex determination in the dioecious *Melandrium*. 1. First lessons from androgenic haploids." *Sexual Plant Reproduction* 3: 179-186.

TW; sex; genetics; chromosomes; Caryophyllaceae; *Silene*; dioecy; cytology; karyosystematics; dimorphism

- Ye, D., Y. Wu, et al. (1992). "On the genetic control of the regeneration response in the dioecious *Melandrium album*." *Sexual Plant Reproduction* 5: 292-297.
TW; *Silene*; Caryophyllaceae; sex; genetics; physiology
- Young, H. J. (2002). "Diurnal and nocturnal pollination of *Silene alba* (Caryophyllaceae)." *American Journal of Botany* 89(3): 433-440.
TW; pollination; Caryophyllaceae; *Silene*; sphingophily; phalenophily; psychophily; melittophily; generalistic; nocturnal; predation; seed; parasitism
Flowers that are open for > 12 h may be visited by both diurnal and nocturnal pollinators. I compared the effectiveness (measured its seed production and pollen movement distance) of diurnal and nocturnal pollinators of *Silene alba*, a species whose flowers open in evening but close by midmorning the following day. By bagging flowers either during evening hours or during daylight hours or both day and night, I compared seed production caused by diurnal and nocturnal pollinators. Flowers exposed only to nocturnal visitors (mostly sphingid and noctuid moths) produced significantly more seeds than flowers exposed only to diurnal visitors (bees, flies, and wasps) Fluorescent dye applied to anthers moved significantly further and to more stigmas at night than during the day. In both measures of pollination effectiveness, nocturnal-visiting moths are better pollinators of *S. alba* than are the diurnal-visiting bees, flies, and wasps. These data support the hypothesis that floral phenology is an adaptation to expose flowers to the most effective pollinators.
- Young, H. J. and L. Gravitz (2002). "The effects of stigma age on receptivity in *Silene alba* (Caryophyllaceae)." *American Journal of Botany* 89(8): 1237-1241.
TW; Caryophyllaceae; nocturnal; anthesis; *Silene*; stigma; senescence; stigma receptivity; dispersal; pollination; efficiency; Apidae; Lepidoptera; mixed pollination; sphingophily; pollinator efficiency; physiology
Silene alba, a perennial, dioecious plant, produces flowers that open in the evening, and can remain open and receptive to pollination for up to 5 d, though in hot and dry conditions the flowers will wilt during the day only to reopen night after night. In the field, it is visited by two different kinds of pollinators with differential success: moths visit the flowers at night, and their movements result in broad pollen dispersal and large seed production, whereas bees, wasps, and flies visit the flowers in the mornings and have decreased pollination effectiveness. However, this differential success may be due to a decrease in stigmatic receptivity soon after the flowers open. We performed controlled pollinations to determine the effect of stigma age on pollen germination and seed set. We pollinated flowers at 12-h intervals up to 120 h and divided these into two sets. From one set, we removed stigmas 24 h after pollination to examine percentage of pollen germination. The second set of flowers was allowed to produce fruits, and the seeds were counted and weighed. Pollen germination declined significantly with stigma age, but there was no significant effect of stigma age at pollination on the number or mass of resulting seeds. Thus, the decreased pollination success of bees is not due to a decrease in stigmatic receptivity but is most likely a result of pollinator inefficiency.
- Zandonella, P. (1966). "Les nectaires des Caryophyllaceae: Présence d'un système de drainage dans le tribu des Lychnideae." *Comptes Rendus des Séances de l'Académie des Sciences, Serie D, Sciences Naturelles, Paris* 262: 2035-2038.
TW; Caryophyllaceae; morphology; nectaries; *Silene*; *Lychnis*; Caryophylloideae
- Zibareva, L., V. Volodin, et al. (2003). "Distribution of phytoecdysteroids in the Caryophyllaceae." *Phytochemistry* 64(2): 499-517.
Silene; Caryophyllaceae; steroid hormones; compounds; chemotaxonomy; phylogeny; seed; root; chemosystematics
Certain genera within the Caryophyllaceae (especially *Silene* and *Lychnis*) have received a significant amount of attention with regard to the isolation and identification of ecdysteroids. However, the taxonomy of this family is difficult. Hence, the occurrence of phytoecdysteroids in members of the Caryophyllaceae is presented, and combined with new data on ecdysteroid agonist (phytoecdysteroid) and antagonist activities, in order to survey the distribution of phytoecdysteroid-containing species within this large family, and to assess the utility of phytoecdysteroids as chemotaxonomic markers. The new data presented (representing ca. 110 species) have been obtained by the application of sensitive biological/biochemical methods for the detection of ecdysteroid agonists and antagonists, using *Drosophila melanogaster* B-II bioassay and ecdysteroid-specific immunoassays. In the antagonist version of the Bit bioassay, only weak ecdysteroid antagonist activities were detected in a few of the extracts. From both new and

previously available data, it was found that phytoecdysteroids were present predominantly in the Genera *Lychnis*, *Petrocoptis*, *Sagina* and *Silene*. Comparison of ecdysteroid occurrence with a molecular phylogeny for the tribe Sileneae [Taxon 44 (1995) 525] revealed close association of ecdysteroid occurrence with certain groups of this tribe. In 14 species of *Silene* examined, there is a reasonable, but not absolute, relationship between the presence of ecdysteroids in the seeds and in other plant parts. Where ecdysteroids are present in the plant, highest concentrations are generally present in the roots. (C) 2003 Elsevier Ltd. All rights reserved.