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Within-population spatial variation in pollinator visitation rates, pollen limitation on seed set, and flower longevity in an alpine species

Sverre Lundemo[a,*], *Ørjan Totland*[b]

[a]*Department of Biology, The Norwegian University of Science and Technology, Realfagbygget, Høgskoleringen 5, N-7491 Trondheim, Norway*
[b]*Department of Ecology and Natural Resource Management, The Norwegian University of Life Sciences, PO Box 5003, N-1342 Ås, Norway*

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ABSTRACT

Pollen limitation through insufficient pollen deposition on stigmas caused by too infrequent pollinator visitation may influence the reproductive outcome of plants. In this study we investigated how pollinator visitation rate, the degree of pollen limitation, and flower longevity varied spatially among three sites at different altitudes within a population of the dwarf shrub *Dryas octopetala* L. in alpine southern Norway. Significant pollen limitation on seed set only occurred at the mid-elevation site, while seed set at the other sites appeared to be mainly resource limited, thus indicating a spatial variation in pollen limitation. There was no association between the spatial variation in the extent of pollen limitation and pollinator visitation rate to flowers. However, pollinator visitation rates were related to flower longevity of *Dryas*; sites with low visitation rates had long-lived flowers and vice versa. Thus, our results suggest within-population spatial co-variation between pollinator visitation rates, pollen limitation, and a developmental response to these factors, flower longevity.

1. Introduction

Pollen availability may affect the female reproductive success of flowering plants (Bierzychudek, 1981; Burd, 1994) through insufficient visitation by pollinators or insufficient transfer of pollen to stigmas per visit (quantity components) and insufficient amount of compatible pollen (quality component) (Bierzychudek, 1981; Zimmerman and Pyke, 1988). Pollen limitation has previously been documented in many species through studies comparing the resulting reproductive success after natural and supplementary pollination with outcross pollen. Burd (1994) found that significant pollen limitation was demonstrated in some years or at some sites in 62% of studied species, indicating that the pollination environment is dynamic and varies spatially and temporarily. Supplementary pollination does not always result in higher female reproductive success compared to natural pollination. On theoretical grounds, Haig and Westoby (1988) showed that when both pollen and abiotic resources constrain seed production simultaneously, seed production should not respond to an increase in pollen supply. This would be the case if the resource availability for some reason were limited by edaphic conditions (i.e. availability of nitrogen, phosphorus or water) or by other environmental

* *Corresponding author.*
E-mail address: sverre.lundemo@bio.ntnu.no (S. Lundemo).
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constraints, such as severe wind, temperature or precipitation conditions.

Flower visitation activity of pollinators is often strongly affected by climatic conditions (McCall and Primack, 1992; Totland, 1994) and the climate varies on both large and small spatial scales. Therefore, it is conceivable that there is variation in pollinator visitation frequency to flowers, both on a large scale among populations and on a small scale within populations (Herrera, 1995; Sullivan and Titus, 1996). This situation could have secondary effects on population-level pollen limitation, resulting in spatial variation in reproductive success based on spatial variation in pollen limitation (e.g. Santandreu and Lloret, 1999). However, even if natural pollen availability, through the activity of pollinators, is spatially constant within a population, there could be spatial variation in the extent of pollen limitation on reproductive success. This is because plants growing in relatively environmentally benign habitats, where physical factors do not constrain seed production, would be capable of responding positively to pollen addition, whereas plants whose seed production is more strongly constrained by physical factors cannot benefit from extra pollen deposition. For example, Totland and Eide (1999) found that plants of an alpine population of *Ranunculus acris* that experienced an experimental increase in growing season temperature responded positively to pollen addition, whereas plants experiencing natural temperatures did not.

Flower longevity, the duration a flower remains open and functional, is an intrinsic feature that could reduce spatial variation in pollen limitation despite spatial variation in pollinator visitation rate. Many flowers wilt after pollination, and the pollination event can thus restrict flower longevity. It has been shown that individual plants may mitigate low pollinator visitation by extending their flower longevity (Bingham and Orthner, 1998; Fabbro and Körner, 2004). It is conceivable that such variation in flower longevity may also occur among plants in different sites of contrasting pollinator visitation rates within a population.

Within-population spatial variation in abiotic resource availability (Lechowicz and Bell, 1991; Jackson and Caldwell, 1993; Gross et al., 1995; Farley and Fitter, 1999) or in weather conditions (Grace, 1988; Rae, 2003) is the rule rather than the exception. Moreover, pollinator visitation rates to flowers often vary considerably among patches within a population, both as a result of spatial variation in weather conditions (e.g. Totland, 1994; Herrera, 1997) and due to spatial variation in floral resource availability (e.g. Totland and Matthews, 1998). However, to our knowledge, very few studies have explored how such spatial variation in the availability of pollinators or abiotic conditions affects levels of pollen limitation on seed production among plants within a population. In this study we examine if spatial variation in pollen limitation occurs within a population of an alpine/arctic insect-pollinated plant, *Dryas octopetala* L. Because alpine species often occur under extreme weather conditions that restrict the activity of pollinators (Corbet, 1990), and pollen limitation often is related to the activity of pollinators, the reproductive success of plants at high altitudes/latitudes is usually thought to be strongly pollen limited (Totland, 1997; Totland and Eide, 1999). We asked (1) if pollinator visitation rate to flowers varied spatially within an alpine population of *Dryas octopetala*, if (2) pollen limitation on seed set occurred, and if so (3), if it varied spatially among sites within the population.

2. Methods

2.1. Study species

Dryas octopetala L. (Rosaceae) is a circumpolar perennial dwarf shrub occurring in contrasting habitats such as tundra, coastal cliffs, sand dunes, mountain meadows, dry slopes and birch forests, often on calcareous soil. The plant forms a mat that produces flowers throughout the growing season. Plants increase their size through clonal growth, and individual clones can live more than 100 years (Crawford, 1989). Flower primordia in *Dryas* are formed during the previous summer, and the hermaphroditic flower consists normally of 8 (seldom 9 or 10) white petals. The sex of each flower can vary from almost pure male with virtually non-existent stigmas to flowers with dominant stigmas and very small anthers. Such gender variation appears to reflect different degrees of environmental stress, with more stressful conditions causing more flowers to become pure male (Wada and Kanda, 2000). This can possibly reflect a condition of andromonoecy or androdioecy in *Dryas* (Wada, 1999). After pollination, the flowers develop many small nuts (achenes) with feather-shaped styles that aid their wind dispersal. *Dryas octopetala* appears to be more or less self- incompatible (McGraw and Antonovics, 1983), and thus require cross-pollination by insects for successful reproduction.

2.2. Study area

We conducted fieldwork during July and August 2003. The study site was situated approximately 1.5 km northeast of Finse, Hardangervidda, Norway (60°36′56″N, 7°31′8″E), on the southwest slope of the mountain Sandalsnuten at ca.1500 m elevation. Sandalsnuten is situated in the mid-alpine vegetation zone, which mostly consists of grass heaths dominated by *Juncus trifidus*, *Carex bigelowii* and *Festuca ovina*. The bedrock in the area consists mostly of phyllite and siliceous schist, with marble from cambro-silurian in scattered patches. This gives rise to rather calcicolous plant communities, where *Dryas* is one of the dominating species, forming so-called *Dryas* heaths. A large population of *Dryas* covers most of the southwest slope of Sandalsnuten. We used three sites along this slope to examine the spatial variation in pollinator visitation and pollen limitation in *D. octopetala*. The lowest elevation site was almost at the bottom of the slope, where there was a transition to grassy heath (ca. 1450 m elevation). The mid-elevation site was at ca. 1500 m elevation, and the highest elevation site was just below the summit (ca. 1550 m elevation). At this site *Dryas* had a more patchy distribution, and the total area covered by *Dryas* mats was distinctly smaller than in the other sites. The sites were about 100–150 m apart and are hereafter denoted low, middle and top site, respectively.

We conducted wind-speed measurements to quantify the spatial variation in environmental severity among our three study sites within the population at Sandalsnuten. The average wind-speed at the top site (3.6 m/s) was always higher