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Original article

Floral herbivory increases with inflorescence size and local plant density in *Digitalis purpurea*

Nina Sletvold[*], *John M. Grindeland*[1]

Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway

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ABSTRACT

Insect herbivores search for their host plants in heterogeneous environments, and the efficiency of host location may be influenced by plant architecture and abundance. In this study, we ask how plant and habitat characteristics traditionally thought to attract pollinators are related to attack rates by floral herbivores. Patterns of floral herbivory by the moth larva *Eupithecia pulchellata* were studied in relation to inflorescence size and local plant density in two years in a natural population of the facultative biennial *Digitalis purpurea*. Overall levels of herbivory were low, 84% of the infested plants lost less than 10% of their flowers. Only 9% of the plants lost more than 20% of their flowers. Probability of herbivory at the plant level increased strongly with inflorescence height, and it was considerably higher in dense patches compared to sparse ones. There was no effect of local plant density on the functional relationship between inflorescence size and probability of herbivory. Both number and proportion of damaged flowers per plant increased with inflorescence height. The results suggest that *E. pulchellata* is attracted to dense patches and large individuals of *D. purpurea*, and that negative effects of herbivory increase with plant size. This implies diminishing returns for investment in more flowers in *D. purpurea*, and indicates that herbivory may select for smaller flowering size and flower number in this monocarpic species.

1. Introduction

The efficiency of host location is an important fitness determinant for insect herbivores. Insect herbivores search for their host plants in habitats where plant architecture, size and density typically vary on a local scale, and herbivores are expected to evolve strategies that deal with high levels of habitat complexity (Cook and Holt, 2006). Host-plant 'apparency' in the habitat should influence location rates (Courtney, 1985), and it is increasingly realized that plant traits usually interpreted in terms of pollinator attraction may affect herbivores and seed predators as well (Herrera, 2000; Ehrlén et al., 2002; Gómez, 2003). One plant trait that may have an effect on both mutualistic and antagonistic interactions is inflorescence size.

The fact that large floral displays attract more pollinators is well established (reviewed by Ohashi and Yahara, 1999), though usually accompanied by a decrease in the proportion

[*] *Corresponding author*. Present address: NTNU, Museum of Archaeology and Natural History, Section of Natural History, N-7491 Trondheim, Norway.
E-mail address: nina.sletvold@vm.ntnu.no (N. Sletvold).
[1] Present address: Sør-Trøndelag University College, Rotvoll Allé 1, N-7004 Trondheim, Norway.
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of open flowers probed (Mitchell et al., 2004; Grindeland et al., 2005). In contrast, little data exist on the relationship between herbivore damage intensity and plant size (Klinkhamer et al., 1997). Several studies have found pre-dispersal seed predation rate to increase with inflorescence size (Traveset, 1994; Ehrlén, 1996; Brody and Mitchell, 1997), indicating that herbivores may select for smaller display size. However, although large plants attract more herbivores, the proportion of flowers or fruits eaten may be a constant (Sperens, 1997) or decreasing (Brody and Mitchell, 1997) function of plant size, indicating selection for large display size.

Herbivore response to variation in host-plant size may also be influenced by local plant density. According to optimal foraging theory, host searching time is expected to decrease with higher host-plant density, and the probability of herbivory in dense populations should increase (Stephens and Krebs, 1986). Empirical results have, however, been mixed (Kunin, 1999; Masumoto et al., 2000; Sheppard and Vitou, 2000; Raghu et al., 2005), and a few studies have reported negative density-dependence (Shea et al., 2000; Bishop, 2002). At present there is little consensus on how insects respond to variation in host density at the patch level (reviewed by Cook and Holt, 2006). Density may also change the shape of the relationship between herbivory and inflorescence size. Rausher (1983) demonstrated that butterflies may alter oviposition behaviour in response to plant density variation, but whether this is a common pattern is unknown. A few, recent studies have found density-dependent response curves in plant–pollinator interactions (Ohashi and Yahara, 2002; Grindeland et al., 2005), but this is largely unexplored in plant–herbivore systems.

This study examines pre-pollination floral herbivory by the geometrid moth *Eupithecia pulchellata* (Geometridae, Lepidoptera) in the facultative biennial *Digitalis purpurea* L. (Plantaginaceae). The moth oviposits on flower buds, and the larva feeds on the anthers and ovaries inside the developing flower. Attacked flowers set no seeds, and flower damage is equivalent to fruit loss. The main objective is to establish how herbivory by *E. pulchellata* is related to variation in inflorescence size in *D. purpurea*. In addition we explore whether local plant density affects damage patterns. The more specific questions addressed are: (1) does probability of floral herbivory increase with inflorescence size, and does plant density at the patch level influence this relationship? (2) Does the proportion of damaged flowers decrease with inflorescence size?

2. Material and methods

2.1. Study system

Foxglove, *D. purpurea* L., is a facultative biennial herb which grows on naturally disturbed soil at places like river banks, heaths, screes and tree uprootings, or on soil disturbed by human activities, as roadsides, wood-clearings and pastures. The species has a persistent seed bank from which abundant germination takes place after soil disturbance (van Baalen, 1982). Seeds mainly germinate in spring, and individuals form basal rosettes that remain vegetative during the first summer. Flowering may occur in the second summer, but delay of flowering for several seasons is common (Sletvold and Grindeland, 2007). The pink to purple, protandrous flowers are produced on terminal racemes from mid June. Flowers open sequentially from bottom and upwards. The length of a population's flowering period is typically 3–4 weeks, but large among-individual differences are found due to variation in total number of flowers (Sletvold, 2002). Plants are self-compatible and primarily visited by bumblebees (Grindeland et al., 2005).

Plants experience herbivory by larvae of the monophagous species *E. pulchellata* Stephens (Geometridae, Lepidoptera), the foxglove pug. This species is restricted to the coastal areas of south-western Norway, following the core distribution of its host plant (Aarvik et al., 2000). Little specific data exist on the field ecology of this species. The moth flies during night in spring and early summer (May–June), and is supposed to be most abundant early in the flowering season of its host plant. Oviposition takes place on immature buds and the larva feeds inside the flowers, consuming the stamens and ovaries (Skou, 1984). The presence of the larva inhibits flower opening, although the ''bud'' grows to a size well beyond the point where it would normally open. There is never more than one larva per flower (J.M. Grindeland and N. Sletvold, unpublished data), suggesting that only one egg is laid on each flower bud. The seed set of damaged flowers is zero.

2.2. Field work

The study was conducted in a pasture at Ulvik (Hordaland County) in south-western Norway. The pasture consisted of a mosaic of areas with varying focal plant density; some areas are disturbed (by grazing/small screes) with high *D. purpurea* density, whereas other areas are closed grassland with low *D. purpurea* density (see Sletvold and Rydgren, 2007 for further details). In 1997 all individuals within an area of approximately 100×5 m on a roadside inside this pasture were selected. Inflorescence height, total number of flowers and presence/absence of *E. pulchellata* were recorded for a total of 394 individuals. On plants where the herbivore was present the number of damaged flowers was determined. This was done during three consecutive days late in the flowering season (mid July). The roadside included areas of both dense and sparse character, but no data on local density were collected.

In 1999, focal plants were chosen within patches of uniform local density, where patch boundaries roughly followed local distribution of *D. purpurea*. From the approximately 450 flowering plants present in the pasture, 14 patches including a total of 133 plants were randomly selected and assigned to two different plant density categories: seven dense patches with plants less than 0.5 m apart, and seven sparse patches with plants more than 1 m apart. Focal plants were haphazardly selected within each patch according to the number available. In dense patches plant number varied from 6 to 14 with a total of 65, and in sparse patches from 8 to 11 with a total of 68. Inter-patch distances varied from 5 to 20 m. Plant height, total number of flowers and presence/absence of *E. pulchellata* were recorded for all individuals. Last recording date was July 8th.