

# Fine-scale spatial genetic structure in predominantly selfing plants with limited seed dispersal: A rule or exception?



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## ABSTRACT

Gene flow at a fine scale is still poorly understood despite its recognized importance for plant population demographic and genetic processes. We tested the hypothesis that intensity of gene flow will be lower and strength of spatial genetic structure (SGS) will be higher in more peripheral populations because of lower population density. The study was performed on the predominantly selfing *Avena sterilis* and included: (1) direct measurement of dispersal in a controlled environment; and (2) analyses of SGS in three natural populations, sampled in linear transects at fixed increasing inter-plant distances. We found that in *A. sterilis* major seed dispersal is by gravity in close (less than 2 m) vicinity of the mother plant, with a minor additional effect of wind. Analysis of SGS with six nuclear SSRs revealed a significant autocorrelation for the distance class of 1 m only in the most peripheral desert population, while in the two core populations with Mediterranean conditions, no genetic structure was found. Our results support the hypothesis that intensity of SGS increases from the species core to periphery as a result of decreased within-population gene flow related to low plant density. Our findings also show that predominant self-pollination and highly localized seed dispersal lead to SGS at a very fine scale, but only if plant density is not too high.

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## 1. Introduction

Restricted pollen and seed dispersal lead to non-random spatial distribution of genotypes in populations. Analysis of spatial genetic structure (SGS) at fine scale (i.e. within populations) allows detecting major gene dispersal distance, the knowledge of which is necessary for efficient species conservation management. According to the theory of isolation by distance, SGS arises from the interplay of limited gene flow and local genetic drift. The rate of decrease of genetic similarity with distance is a measure of strength of SGS (Loiselle et al., 1995; Rousset, 2000; Hardy, 2003). How strength of SGS relates to the biology of the species and the degree of inter- and intra-specific variation in this property is an important question of population genetics (Vekemans and Hardy, 2004; Jump et al., 2012). The extent of SGS within plant populations depends not only on seed and pollen dispersal distance but also on breeding

type, level of self-fertilization and effective plant density (Vekemans and Hardy, 2004). In species with more restricted pollen dispersal, lower gene flow is expected to result in higher genetic differentiation, and therefore self-fertilizing species are expected to have both smaller effective population sizes (Ingvarsson, 2002) and lower pollen movement leading to higher genetic structure than out-crossing species (Hamrick and Godt, 1996). Higher SGS is also expected in more patchy and peripheral populations because of lower plant density, smaller population sizes, and lower intensity of gene flow (Doligez et al., 1998; Vekemans and Hardy, 2004). Although still limited, there are an increasing number of reports on SGS in fragmented versus continuous (Williams et al., 2007; Born et al., 2008; De-Lucas et al., 2009) and core versus peripheral populations (Gapare and Aitken, 2005; Pandey and Rajora, 2012; Meeus et al., 2013; Volis et al., 2014).

Here we investigate gene dispersal patterns in an annual grass *Avena sterilis*. This species is well-suited for studying fine-scale gene flow and SGS in a predominantly self-fertilizing plant. It has a wide range with often almost continuous local distribution which allows sampling at specified distances. At the same time, while core populations are large and dense, peripheral populations are usually

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smaller, more isolated and patchily distributed. Our study employed (1) direct measurement of seed dispersal in a controlled environment; and (2) analyses of SGS in 3 natural populations of *A. sterilis* representing different ecological conditions and species range positions, sampled in linear transects at fixed increasing inter-plant distances.

Our hypotheses were: (i) since *A. sterilis* is predominantly (>95%) self-pollinated with gravity-dispersed seeds, this species is expected to have fine-scale within-population SGS; (ii) the peripheral populations of the species are expected to have higher levels of SGS than the core populations due to their lower population size and density; and potentially more restricted gene dispersal.

## 2. Materials and methods

### 2.1. Study species

*A. sterilis* L. is a winter annual, and a predominantly self-pollinating grass (Phillips et al., 1993). This species is one of the major components of annual vegetation throughout Israel. It forms massive stands in the mesic Mediterranean including open park-forests, maquis and hemicyptophytic/dwarf shrub formations, and also penetrates into favorable desert habitats (wadi beds and loessy depressions) (Harlan and Zohary, 1966; Zohary, 1983).

In this species the inflorescence is a panicle. Upon maturation the whole spikelet (comprising two to four florets) disarticulates and acts as a drill-type dissemination device. The fallen spikelets either are impaled in the dry remnants of the dead mother plant or penetrate into soil cracks by the combined effects of wind and gravity (Volis personal observations), where they remain until germination the following season. Spikelets are intensively harvested by ants and granivorous rodents (Volis personal observations). Seeds that do not germinate in the autumn following dispersal either die or enter the soil seed bank where they can remain dormant for several years (Volis, 2012, 2014).

### 2.2. Sampling

The sampling design followed Volis et al. (2010). Seeds were sampled in nine linear transects at fixed distances (0, 1, 2, 5, 10, 20, 50, 100 and 400 m) at three population locations in Israel, representing three distinct environments and vegetation communities: Mediterranean grassland (AM), shrub and semi-shrub association called batha (BG), and desert (SB). The Mediterranean grassland location (AM population) was in the Upper Galilee, 1 km west of Kibbutz Ammiad (elevation 300 m, annual precipitation around 600 mm). The batha location (BG population) was in Beit Guvrin National Park located in the Shefela Hills (elevation 300 m, annual precipitation 400 mm). The desert location (SB population) was in a wadi in the Negev Desert (elevation 400 m, annual precipitation 90 mm) (Fig. 1).

In addition, population locations differed in their position within a species distributional range, representing either species core (AM and BG) or periphery (SB). For genetic analysis, seeds were germinated and grown to the two-leaf stage.

### 2.3. Population demography

Average plant density was estimated in two of three populations (SB and BG) during 1996–1999. In 1996, six 10-m transects, distributed along a slope 20 m apart, were marked in the BG location. Five 1 m<sup>2</sup> plots 1 m apart were permanently marked along each transect. At this site, the distribution of *A. sterilis* was more or less continuous. At the SB location, where vegetation distribution

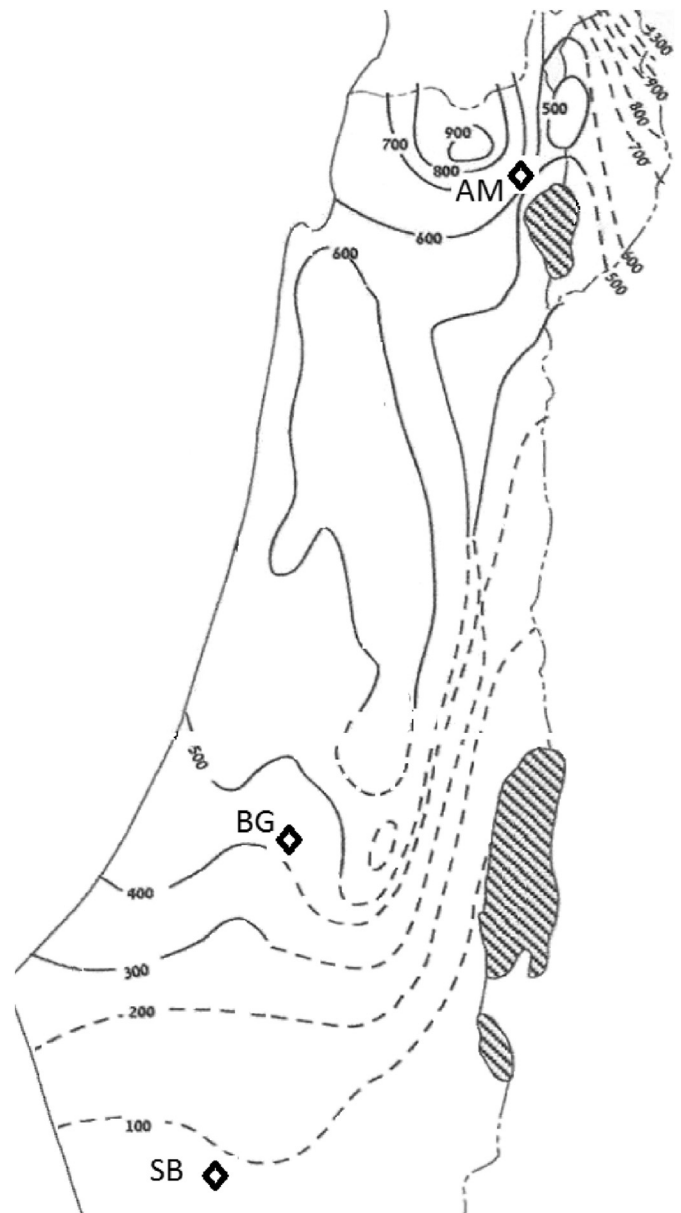


Fig. 1. Map of Israel showing isohyets of multiyear averages of annual rainfall amount (mm) and study populations.

was sparse and patchy, neither transects nor equidistant spacing was possible. Therefore, 1 m<sup>2</sup> plots were marked in 1996 in each vegetation patch containing oat plants. Altogether, 30 and 50 plots were marked at the SB and BG locations, respectively. The higher number of plots at the SB location was due to the higher spatial heterogeneity at this location compared with the BG location. During the next four years, adult plants and number of seeds per plant were counted in each plot. In 1996, plant fecundity was estimated at both locations, but plants per plot were counted at SB location only. In 1999, because of very low amount of rainfall, no plant reached adulthood in the SB population, and there was no estimate of plant density.

### 2.4. Seed dispersal experiment

The effects of wind and gravity on seed dispersal distance in *A. sterilis* were tested as described in Volis et al. (2010). Two

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