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VARIATION OF REPRODUCTION IN SOME SPECIES OF THE TRIBE AVENEAE (POACEAE)

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Abstract. Patterns of reproduction were studied in a series of inter- and intraspecific units in the genus *Avena*. The range of variation of the mating system is from autogamy to allogamy. The first system is expressed in cultivated types, while the second is observed in wild and weedy ones. In a wild oat of putative hybrid origin or being a mutation, the development of pollen grains deviates from that noted in grasses as normal.

Key words: Aveneae, anther morphometry, autogamy, allogamy

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Introduction

Considerations on breeding or mating systems are of fundamental importance for the study of variability of plants. Not only the patterns of trait genetic variation but also the range of phenotypic plasticity depends on the level of allo- or autogamy. Recognition of the mating system is difficult, because the structure of the flower, e.g., the relationships between the female and male organs, change distinctly under the influence of various environmental factors. In the tribe Aveneae Dumort., polymorphism of flowers within one spikelet exists, presenting various sex expression. This additionally complicates the analysis. The level of outcrossing in *Avena barbata* Pott ex Link has been estimated at 2% (Jain 1975), while in *A. fatua* L. it varies between 1 and 13% (Grant 1981). One can also expect that in the genus *Helictotrichon* Besser the outcrossing rate will be variable depending on size of the lodicules. For instance, *H. leve* (Hack.) Potztal has a large lodicule with a thick cushion, while *H. albinerve* (Boiss.) Henrard has it small with a very slim cushion (Röser 1989). Thus, *H. leve* has greater potential for outcrossing, because its lodicules can open flowers (chasmogamy). The energetic effort of outcrossing plants is very high. Such plants produce many pollen grains (ca 5859 grains per ovule) while in cleistogamic flowers it amounts to only 28 grains (Grant 1981). Since in grasses the anther development is original, so an increase in pollen grains amount appears as an elongation of the anther (Batygina 1987; Niklas 1994; Kosina & Florek 2011). Such developmental interrelationships were documented in the genera *Bromus* L. and *Secale* L. (McKone 1989; Hammer 1990).

Material and methods

Sixteen operational taxonomic units (OTUs) belonging to ten taxa of the tribe Aveneae were described by three characteristics of anther. Intratribal and intraspecific units (species, subspecies, an intermediate form *sterilis* - *ludoviciana*) and their symbols (in brackets) used in the text and diagram are as follows: *Avena longiglumis* Durieu (Al), *A. strigosa* Schreb. (As1, As2), *A. barbata* Pott ex Link (Ab), *A. ×sativa* L. (Asa1, Asa2), *A. fatua* L. (Af), *A. sterilis* L. ssp. *ludoviciana* (Durieu) Gillet et Magne (Asl1, Asl2), *A. sterilis* ssp. *sterilis* - ssp. *ludoviciana* (Ass-l), *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl et C. Presl. (Ae1, Ae2, Ae3), *Avenula planiculmis* (Schrad.) W. Sauer et Chmel. (Ap1, Ap2, Ap3).

All these accessions were cultivated under equal soil-climatic conditions on small plots in the grass collection of the author. Then, the material of the study was treated as a design of the completely randomised one-way classification. Three traits were evaluated for each accession: the number of pollen grains per anther, length of anther and diameter of pollen grain. Viability of pollen grains with application of acetocarmine was estimated for all accessions, and additionally for *Helictotrichon parlatorei* (J. Woods) Pilg. The OTUs were arranged into an ordination space with application of non-metric multidimensional scaling (Kruskal 1964; Rohlf 1981) and according to Rohlf's numerical approach (Rohlf 1994).

Results and discussion

It was proved that the two methods applied for evaluation of pollen grain viability by acetocarmine and germinability by fluorescein diacetate staining, are highly correlated (Platje 2003). The highest pollen grain viability (100%) was noted in *Arrhenatherum elatius*, though some of its types expressed 5% of dead grains. The same percentage of dead grains was also observed in *Avenula planiculmis*. In *Helictorichon parlatorei* dead grains amounted to 14%. The development of some pollen grains, e.g. in *Avena fatua* and *A.* ×*sativa*, can be stopped in the stage of one nucleus and such pollen do not germinate (Warzych 2001). Such development can be caused by anomalous cytokineses in the monolayered microspore mother cells in the pollen sac (Kosina & Florek 2011). The non-viable pollen grains were small, without starch grain storage, with one or two nuclei. The length of the anther was highly positively correlated with the number of grains per anther, and both traits were negatively correlated with the diameter of pollen grain.

A numerical analysis was made for a set of OTUs, using an average taxonomic distance matrix, which is an initial one in the non-metric multidimensional scaling method. A very low value (0.003) of a stress 2 coefficient shows a very good fit between the initial matrix and distances between OTUs in a configuration space. Results are presented in Fig. 1. The largest values of ordination axes x and z are noted for a set of three OTUs, Ae2, Ap3 and Ass-l. They have the longest anthers, the highest number of pollen grains per anther and the smallest diameter of pollen grains. For instance, Ae2 has 5.4 mm long anthers, 9200 pollen grains per anther and only 120 relative units of a grain diameter. In the set of OTUs, some hybrid (?) form of weedy oats, *Avena sterilis* ssp. *sterilis* - ssp. *ludoviciana* creates a cluster together with two wild species, *Arrhenetherum elatius* and *Avenula planiculmis*. The longest anthers were expressed in *Avenula planiculmis* (Ap1), which is in an intermediate cluster together with Ae1. Another intermediate cluster includes wild *Aveneae* members (Ae3, Ap2) and two diploids of *Avena*, a wild *A. longiglumis* (Al) and a weedy-cultivated *A. strigosa* (As1). On the right side of the diagram, an extreme OTU Asl1 is located. Its characteristics are as follows: anthers 2.5 mm long, 1750 pollen grains per anther, grain diameter 251 relative units. Two poles are distinct in the diagram, for auto- and allogamy. Allogamy is mainly expressed in wild units, *Arrhenatherum elatius* and *Avenula planiculmis*, but also in some form of possible hybrid origin, Ass-l. Ass-l has an intermediate gross morphology between two subspecies of *Avena sterilis* ssp. *sterilis* and ssp. *ludoviciana*. This OTU has long anthers (5.5 mm) with many grains in pollen sacs (8120 grains per anther) and these grains are the largest (361 relative units of diameter). The known negative correlation between the number of pollen grains per anther and their diameter is broken here. This oat produces many and very large pollen grains. Its energetic reproduction effort is very high. Such development can be explained in two ways: the plant reached high but optimal level of polyploidy or it is a natural mutation. Of these, the second explanation is more probable. Giant pollen grains having many pores have been discovered in oat amphiploids (Kosina *et al.* 2014). These anomalous grains have weaker germination when compared to normal pollen grains. A tendency to allogamy was also discovered in oat fatuoids (Warzych 2001). Taxonomic units expressing autogamy belong mainly to cultivated or weedy forms of *Avena*. *Avena*

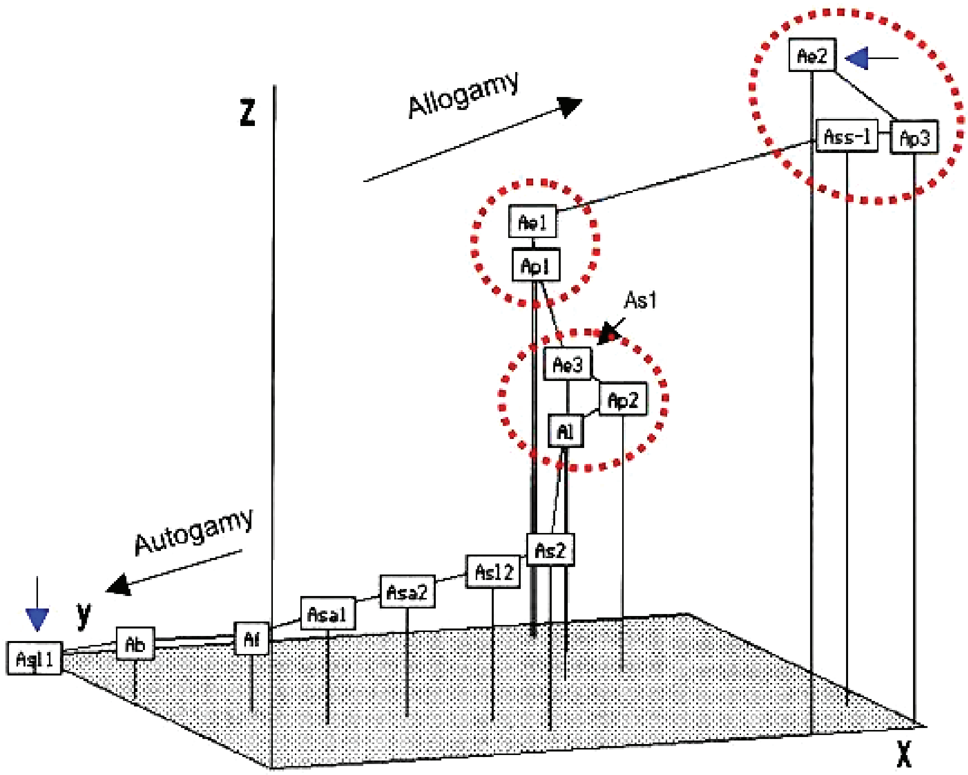

Fig. 1. Minimum spanning tree of species and subspecies of the tribe Aveneae in an ordination (configuration) space created by the non-metric multidimensional scaling method, presenting the variation in the breeding system – autogamy *versus* allogamy.

longiglumis is an intermediate type between both types of reproductive behaviour.

Avena fatua, a common weed in cereal cultivation, is among the autogamic units. Some of its forms can even express cleistogamy with pollen grains germinating in anther sacs. This species is also highly polymorphic and this variability is remarkable in its spikelet and flower structure as well as in pollen grains germinability (Warzych 2001).

A range of reproductive behaviour between auto- and allogamy was also shown in the genus *Brachypodium* P. Beauv. with extremes *B. distachyon* (L.) P. Beauv. *versus B. pinnatum* (L.) P. Beauv. (Kosina & Kłyk 2011) and in the genus *Bromus* L. with extremes *B. trinii* É. Desv. *versus B. arvensis* L. (Kosina & Szmidzińska 2000). The breeding behaviour is distinctly influenced by environmental conditions and, for instance, autogamy can be changed into facultative allogamy when flowers are opened under suitable weather, such as it was documented in *B. distachyon* (Kosina & Tomaszewska 2012).

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