

Fertility and Viability of Pollen Grains of *Taraxacum officinale* Wigg. s.l. (Asteraceae, Magnoliopsida) in a Gradient of an Anthropogenically Transformed Environment

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Abstract—The fertility and viability of pollen grains of two morphological forms of *Taraxacum officinale* Wigg. s.l. were estimated. These forms compose common coenopopulations growing in various coenotic and edaphic conditions. The forms studied possess developed gynoeceia—a large number of fertile pollen grains capable of germinating under certain temperature conditions. This fact points to the amphimictic properties of the plants. Comparison of the data on the fraction of fertile pollen grains and seed productivity allows assuming that some seeds develop without fertilization. This can be considered as evidence of the apomictic properties of plants. Therefore, the presence of facultative apomixis in the species considered was confirmed indirectly in our work. The fertility of pollen grains was shown to be a characteristic of the male gametophyte that was more environmentally dependent than its viability. Under favorable conditions, the share of fertile pollen grains in f. *dahlstedtii* and f. *pectinatiforme* differ insignificantly. Under stress, the differences between the dandelion forms by this index increase. This can be considered as a mechanism of adaptation to adverse environmental factors. The revealed differentiation of the morphological forms of dandelions by the index of pollen grain fertility suggests that edaphic and coenotic stresses increase the differences between them in the degree of apomictic and amphimictic properties. The morphological forms of dandelions, by realizing two reproductive strategies under stress, ensure both the abundance and the genetic heterogeneity of the coenopopulations. The morphological forms studied do not differ in the proportion of viable pollen grains. This index increases in the gradient of coenotic competition only to a certain extent, which can be considered as a manifestation of the properties of the facultative apomict.

Keywords: *Taraxacum officinale*, male gametophyte, fertility and viability of pollen grains, coenotic and edaphic conditions

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INTRODUCTION

The possibility of a stable existence of coenopopulations under environmental stress is provided by their various properties, including the lability of the reproductive sphere of plants. A significant number of publications have been devoted to this problem, in which the influence of weather, edaphic, and other external conditions on the abundance and viability of seed offspring is discussed in detail (Elkarmi and Eideh, 2006; Calabrese, 2008; Zvereva et al., 2010; Pozolotina et al., 2012, 2016; Shimalina et al., 2017). Significantly fewer studies have been devoted to the state and viability of the male gametophyte of plants under these condi-

tions (Tret'yakova and Noskova, 2004; Foster and Afonin, 2005; Kisternyi and Panicheva, 2012; Tupitsyn et al., 2012; Ereshenko, 2014; Korshikov et al., 2015). Usually, the issue of the pollen of woody plant species and the influence of the growing conditions on its quality is considered in the available papers. The morphological and functional states of the male gametophyte of herbaceous plants, including those growing under the conditions of anthropogenic transformation of the environment, have been investigated in fewer studies (Zhuikova et al., 2007; Ivanov et al., 2009; Konchina and Yashina, 2015).

The common dandelion (*Taraxacum officinale* Wigg. s.l., 1964), a species of the genus *Taraxacum* Wigg. of the family Asteraceae Dumort (Compositae Giseke) (Cherepanov, 1995), was chosen as the object of our research. This species has a Eurasian type of range (*Flora SSSR ...*, 1964; Rothmaler, 1972). *T. officinale* is a facultative apomictic species (Ermakova, 1990). In most plants, autonomous unreduced parthenogenesis is observed, which is not the primary absolutely obligate form of reproduction. The species is polymorphic. The group of microspecies of *T. officinale* Wigg. s.l. includes both pollen-free forms and forms that have pollen (Plisko, 1969). Previously, we found that two morphological forms—*T. off. f. dahlstedtii* Lindb. fil. and *T. off. f. pectinatiforme* Lindb. fil.—are represented in the structure of *T. officinale* Wigg. s.l. coenopopulations in the Tagil region of the Middle Urals (Bezel et al., 1998). Data on the fertility and viability of pollen grains of the studied species are limited and sometimes contradictory (Poddubnaya-Arnoldi, Dianova, 1937; Plisko, 1969; Zhuikova et al., 2007).

The purpose of this work is a comparative assessment of the fertility and viability of pollen grains of two morphological forms of *Taraxacum officinale* Wigg. s.l. growing under different coenotic and edaphic conditions, including soil pollution with heavy metals.

The following hypothesis is discussed: in a gradient of coenotic conditions and technogenic transformation of the environment, this species may have morphological forms differing in the level of fertility and viability of pollen grains, which reflects its adaptation to contrasting environmental conditions.

Compared to our previous study (Zhuikova et al., 2007), in this work we used more accurate methods for assessing the proportion of fertile pollen grains in the study areas. Statistical data analysis, instead of the one-way analysis of variance, was performed using the modern method of generalized linear models, which takes into account several factors as well as their interactions.

MATERIALS AND METHODS

The functional state of the male gametophyte of two morphological forms of *T. officinale* was studied on background and technogenically transformed territories. The material was collected in the period of mass flowering of the species (first ten-day period of June 2017) in five coenopopulations growing on deposits and dumps of industrial enterprises. The study area was the taiga geographical zone, a subzone of the southern taiga (the Tagil region of the Middle Urals, 58° N, 60° E).

Given the complex of the physicochemical parameters of soils, two groups—agrozems (A) and technozems (T)—were distinguished. In accordance with the soil group, the sites on which various herbaceous phytocenoses grow were designated as A-1, A-2 and T-1,

T-2, T-3. This series of sites represents the gradient of soil pollution with heavy metals (HMs), the integrated index of which is the total toxic load (Z, rel. units). The main soil parameters are summarized in Table 1. Agrochemical indices are presented for the root layer (horizon P on agrozems and horizon AY on technozems).

Soils of sites A-1 and A-2 were similar in the agrochemical characteristics and favorable for *T. officinale*, which is an eutroph. It grows abundantly in ecotopes provided with nutrients (Hofsten, 1954; Rabotnov, 1956) and rich in nitrogen (level 7 of the Elenberg scale) (Hofsten, 1954). The absence of one of these elements depresses the plant. It occurs at pH from 4.8 to 7.2 (levels 5 and 7 of the Elenberg scale); however, a soil solution close to neutral is optimal (Hofsten, 1954). As a mesophyte, it is abundant only on moderately and strongly moistened soils (level 5 of the Elenberg scale) and grows poorly in stony and droughty areas.

The soils of technozems are more heterogeneous in terms of the agrochemical indices and less favorable for dandelions. The sites studied do not form a clear gradient in the content of nutrients. In terms of the acidity of the soil solution, sites T-2 and T-3 are unfavorable for dandelions.

Syntactic status of communities: A-1, rankless community *Elytrigia repens* [*Stellarietea mediae/Molinio-Arrhenatheretea*]; A-2, rankless community *Carum carvi*—*Festuca pratensis* [*Arrhenatherethalia*]; T-1, rankless community *Trifolium pratense*—*Festuca pratensis* [*Arrhenatheretalia*]; T-2, rankless community *Tussilago farfara*—*Calamagrostis arundinacea* [*Dauco-Melilotion/Agropyron repentis*]; T-3, rankless community *Lathyrus pratensis*—*Calamagrostis arundinacea* [*Dauco-Melilotion/Agropyron repentis*].

The herbaceous communities considered are serial, forming on deposits and dumps. In these territories, their development goes in the direction of increasing species richness and total projective cover of plants, which reflects the degree of development of competitive coenotic relations. Such changes are typical for reductive succession (Whittaker, 1980; Mirkin et al., 2001). On the basis of these parameters and taking into account the floristic composition of phytocenoses, their succession age was determined.

Species richness of the agrozem communities (pcs.): A-1, 25; A-2, 50; the total projective cover (%): A-1, 103.1; A-2, 137.7. Taking into account the floristic composition, this allowed us to present the following gradient of the succession age of the communities, which coincided with the gradient of coenotic competition: A-1→A-2. On the technozems, the number of species in the community of site T-1 was 47, T-2, 42; T-3, 32; the total projective cover: T-1, 148.4; T-2, 82.9; and T-3, 76.8%. By the floristic composition, the community of site T-1 belongs to the meadow stage, and the communities of sites T-2 and T-3 belong

Table 1. Agrochemical indices and the content of mobile forms of HMs in soil (data are represented as the mean values and the standard error of the mean, $n \geq 10$)

Indices	Soil group				
	agrozem		technozem		
	A-1	A-2	T-1	T-2	T-3
	57°57'50" N, 60°15'11" E	58°12'25" N, 60°30'12" E	57°58'13" N, 59°58'35" E	57°54'14" N, 59°54'41" E	57°58'12" N, 59°57'21" E
Agrochemical indices*					
pH _{aq}	6.55	6.32	6.76	7.63	7.35
V, %	90.55	84.62	95.14	98.19	97.97
N _{easy} , mg/100 g	5.10	5.61	4.76	4.14	5.12
P ₂ O ₅ , mg/100 g	19.31	3.68	34.34	69.59	4.25
K ₂ O, mg/100 g	20.05	22.39	38.97	57.79	55.69
C _{tot} , %	3.59	4.48	6.69	3.57	5.52
HM content in soil, µg/g**					
Cd ²⁺	0.1 ± 0.02	0.13 ± 0.02	0.9 ± 0.10	1.5 ± 0.50	2.82 ± 0.44
Co ²⁺	6.5 ± 0.90	0.22 ± 0.01	14.5 ± 3.60	124.2 ± 17.80	–
Cr ³⁺	13.1 ± 0.80	36.31 ± 1.76	7.8 ± 1.10	7.1 ± 2.30	51.90 ± 3.44
Cu ²⁺	12.6 ± 0.90	7.35 ± 0.78	101.6 ± 11.10	951.5 ± 36.10	194.60 ± 6.60
Fe ³⁺	788.9 ± 50.90	376.62 ± 6.84	841.1 ± 13.20	13721.0 ± 670.60	2736.60 ± 85.36
Mn ²⁺	291.6 ± 27.20	–	375.2 ± 54.00	2364.9 ± 93.50	–
Ni ²⁺	13.0 ± 0.90	–	7.4 ± 1.40	7.8 ± 1.30	–
Pb ²⁺	8.1 ± 0.90	7.94 ± 2.33	38.80 ± 4.90	12.4 ± 3.90	193.85 ± 18.34
Zn ²⁺	17.5 ± 1.60	59.44 ± 3.07	262.7 ± 39.6	391.0 ± 125.90	850.40 ± 18.26
Z, rel. units.	1.0	1.47	6.19	22.78	30.00

pH_{aq}, pH of an aqueous solution; V, saturation with bases; N_{easy}, nitrogen of easily hydrolyzable compounds; C_{tot}, total carbon of the soil; dash, data not available. Compiled by * Zhuikova et al., 2015; ** Ivshina et al., 2014.

to the cereal stage of succession. The differences in the species richness and projective cover of the communities of sites T-2 and T-3 were apparently related to the adverse edaphic conditions of the latter. In characterizing the considered series of the phytocenoses of these territories, it is more accurate to speak only of the gradient of coenotic competition: T-3 → T-2 → T-1. This gradient reflects an increase in the projective cover and increased competition. On agrozem, the gradient of coenotic competition coincides with the gradient of the toxic load, whereas on technozem they are the opposite. Thus, there were two stressful situations on technozem within the areas considered, one of which was associated with a high level of coenotic competition (coenotic stress), and the other of which was associated with a high pH and heavy metal content (edaphic stress). Plants growing within agrozem were subject only to coenotic stress, whereas the edaphic conditions in these sites fall within favorable limits.

During the work, one calathid was collected from ten individuals of each morphological form of dande-

lions in the same flowering phase in the coenopopulations studied. Plants located at a distance of at least 3–5 m from one another were selected randomly. In total, 100 inflorescences were collected and placed in individual paper bags with the corresponding labels. All further analysis was performed on freshly collected material.

The *pollen grain fertility* was determined by the standard acetocarmine procedure (Pausheva, 1988). Pollen grains were placed on a glass slide on the surface of a drop of acetocarmine and covered with a coverslip. The preparation was heated over an alcohol lamp for 3–5 s. Pollen grains were examined with a Mikmed 5 microscope (JSC Lomo, Russia) at a magnification of ×120. The fertility of pollen grains was assessed by their color: pollen grains of dark red and burgundy color were classified as fertile. For each preparation, the number of fertile and sterile grains was counted in ten fields of view of the microscope. The proportion of the fertile pollen grains in the site

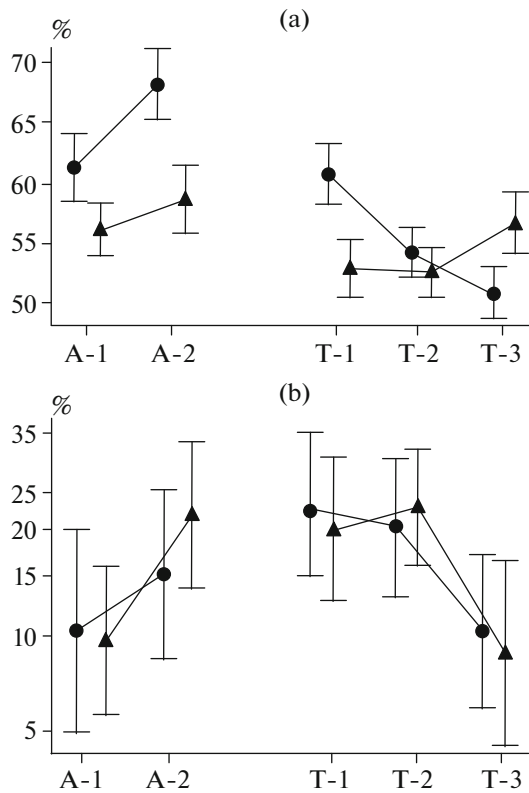


Fig. 1. (a) Fertility and (b) viability of pollen grains in plants from the studied coenopopulations: (▲) *f. dahlstedtii*, (●) *f. pectinatiforme*. Bars show a 95% confidence interval.

was defined as the weighted average of the number of pollen grains in all fields of view per plant.

The *pollen grain viability* was determined by the hanging drop procedure in a moist chamber (Schwartzman, 1986; Pausheva, 1988). Previously, the sucrose concentration most effective for assessing the pollen grain viability was determined. For this purpose, five pollen preparations were prepared simultaneously from each plant. Pollen was shaken off into a drop of sucrose solution at concentrations of 0.1, 1.0, 5.0, 10, and 20%. Previously, it was established that the pollen grains of the morphological forms of dandelions studied do not germinate at room temperature (20–25°C) (Zhuikova et al., 2007). With this in mind, the preparations were incubated in a thermostat at 30°C for 60 min. Then, the number of grains with pollen tubes was counted in five fields of view of the microscope for each preparation (magnification, $\times 120$). In total, 2500 fields were viewed.

Preliminary analysis showed that only low concentrations (0.1 and 1.0%) were effective. Taking into account the absence of differences in the proportion of viable pollen grains in sucrose solutions at these concentrations ($p > 0.05$), only the data obtained at a sucrose concentration of 0.1% were included in the analysis.

The morphological form of dandelions and the group of soils (agrozeems and technozeems), within which the sites differed in agrochemical indices, the content of heavy metals in the soil, and the succession age of the communities, were considered as factors affecting the studied indices of the functional state of the male gametophyte.

To analyze the effect of these factors on the fertility and viability of pollen grains, we used generalized linear models (GLMs). Since the dependent variable has a binomial distribution, we used a logistic regression. In our model, categorical independent variables are represented by vectors with codes. In particular, the predictor “agrozem” has a value of “zero,” and “technozem” has a value of “unity.” Statistical data analysis was performed in the R software (R Core Team, 2017).

RESULTS

Fertility of pollen grains of *T. officinale*. The change in the proportion of fertile pollen grains in plants of the two morphological forms of dandelions growing in the gradients of the factors considered is shown in Fig. 1. The studied index of *f. pectinatiforme* is significantly higher on agrozeems than on technozeems (on average, 65 vs 55%, respectively), whereas in *f. dahlstedtii* the index within the soil groups studied differs nonsignificantly (57 vs 54%). In general, the proportion of fertile pollen grains in the dandelion forms studied on agrozeems is higher than that on technozeems.

The revealed differences are based on the frequency of occurrence of families with different proportions of fertile pollen grains in coenopopulations (Fig. 2). Plants with this index greater than 60% play a major role in reproduction (vertical line in Fig. 2). On agrozeems, the frequency of occurrence of plants with such a fraction of fertile pollen for *f. pectinatiforme* and *f. dahlstedtii* was 70 and 40%, respectively; on technozeems, it was only 44 and 26%, respectively. When analyzing the results, we first assessed the effect of the morphological form and soil composition of the combined samples of all agrozem sites and all technozem sites on the fertility of *T. officinale* pollen grains. A significant effect of the factors “soil group” and “dandelion form,” as well as their interaction ($p \leq 0.05$) (Table 2), on the index studied was established.

Next, we performed a GLM analysis of the pollen grain fertility separately for agrozeems and technozeems. It was shown that, in the first case, the level of fertility differed statistically significantly only between the morphological forms of dandelions (Table 2). An increase in the proportion of fertile pollen grains upon the transition from site A-1 to A-2 was noted only at the trend level. On technozeems, the effect of all the factors considered was statistically significant. The combined effect of the factors “site \times form” on the fertility of pollen grains of plants was observed only on the technozem sites (Table 2).

Pollen grain viability. The results of the study of the proportion of viable pollen grains are shown in Fig. 1b. On agrozoems, the index studied in *f. dahlstedtii* was 10 and 22% (for A-1 and A-2, respectively); in *f. pectinatiforme*, it was 10 and 15%. For technozems, the changes in the pollution gradient were more significant: 9–23% (*f. dahlstedtii*) and 10–23% (*f. pectinatiforme*).

The effect of the factors “soil group” and “dandelion form,” as well as their interaction, on the pollen grain viability was nonsignificant ($p > 0.05$, Table 3). Only the factor “site” had a significant effect on this index.

DISCUSSION

It is known that *Taraxacum officinale* is a facultative apomictic species with amphimictic and apomictic properties. Our study showed that *f. dahlstedtii* and *f. pectinatiforme* have a developed gynoeceum—a large number of fertile pollen grains capable of germinating under certain temperature conditions. This fact indicates the presence of amphimictic properties in the plants. To confirm the apomictic properties of the morphological forms studied, the assessment of the pollen grain fertility was compared with the data on the seed productivity of plants growing in the background zone sites for the same growing period. For this purpose, in the period of mass ripening of fruits, we determined the proportion of full-fledged seeds in the calathid in ten plants from each coenopopulation.

It was found that a decrease in the proportion of fertile pollen grains in plants on sites A-2 → A-1 (see Fig. 1) is not accompanied by a decrease in the pro-

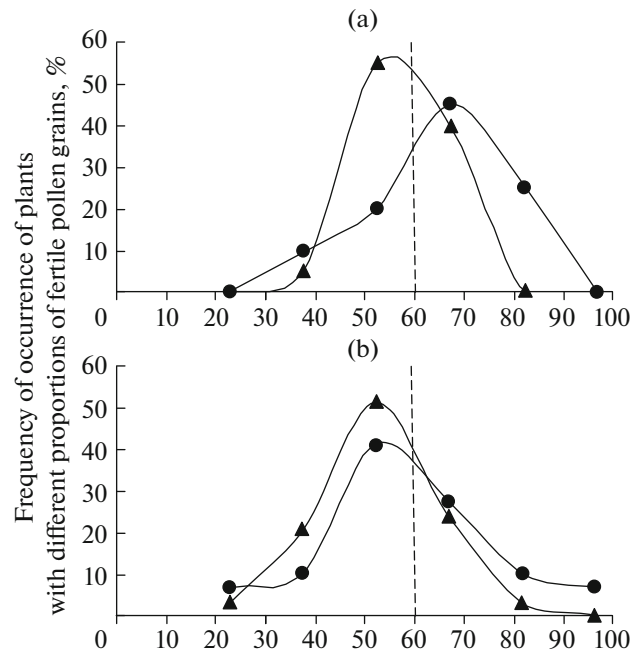


Fig. 2. Frequency of occurrence of plants *f. dahlstedtii* (▲) and *f. pectinatiforme* (●) with different proportions of fertile pollen grains ((a) agrozoems, (b) technozems).

portion of full-fledged seeds in the calathid (96.5 and 96.1%, respectively, in *f. dahlstedtii* and 94.5 and 94.8%, respectively, in *f. pectinatiforme*). This fact suggests that the development of at least part of the seeds on site A-1 occurred without the involvement of a male gametophyte, i.e., without fertilization. This can be considered as indirect evidence that the studied

Table 2. Influence of factors “soil group” (agrozoems or technozems) and “morphological form” on the fertility of pollen grains of *T. officinale*

Factor	Estimates	Standard error	<i>p</i>
Proportion of fertile pollen grains by soil groups and dandelion forms			
Soil group (technozems)	-0.139	0.046	<0.01
Dandelion form (<i>f. pectinatiforme</i>)	0.313	0.057	<0.01
“Soil group × Form”	-0.267	0.069	<0.01
Proportion of fertile pollen grains by sites and dandelion forms within agrozoems			
Plot (A-1)	-0.100	0.077	0.19
Dandelion form (<i>f. pectinatiforme</i>)	0.394	0.087	<0.01
“Plot × form”	-0.183	0.116	0.11
Proportion of fertile pollen grains by sites and dandelion forms within technozems			
Plot (T-1)	-0.154	0.071	<0.01
Plot (T-2)	-0.169	0.068	<0.01
Dandelion form (<i>f. pectinatiforme</i>)	-0.239	0.071	<0.01
“Plot (T-1) × Form”	0.560	0.100	<0.01
“Plot (T-2) × Form”	0.310	0.092	<0.01

A significant effect of factors is highlighted in bold.

Table 3. Effect of the factors “soil group” and “morphological form” on the viability of pollen grains of *T. officinale*

Factor	Estimates	Standard error	<i>p</i>
Proportion of viable pollen grains by soil groups and dandelion forms			
Soil group (technozems)	0.288	0.258	0.26
Dandelion form (<i>f. pectinatiforme</i>)	−0.089	0.324	0.78
“Soil group × Form”	0.038	0.396	0.92
Proportion of viable pollen grains by sites and forms growing within agrozems			
Plot (A-1)	−0.977	0.413	< 0.05
Dandelion form (<i>f. pectinatiforme</i>)	−0.467	0.439	0.29
“Plot × Form”	0.541	0.661	0.42
Proportion of viable pollen grains by sites and forms growing within technozems			
Plot (T-1)	0.970	0.470	< 0.05
Plot (T-2)	1.139	0.435	< 0.05
Form (<i>f. pectinatiforme</i>)	0.170	0.479	0.72
“Plot (T-1) × Form”	0.007	0.625	0.99
“Plot (T-2) × Form”	−0.327	0.597	0.58

forms growing on the territory of the Tagil region of the Middle Urals possess apomictic properties. The advantage of apomicts is the high seed productivity, often independent of pollination and fertilization (Atabekova and Ustinova, 1987).

The results obtained confirm the ideas expressed in the literature about the facultative apomixis in dandelions (Poddubnaya-Arnol'di and Dianova, 1937; Plisko, 1969; Ermakova, 1990; ZhuiKOVA et al., 2007) and allow considering the proportion of fertile pollen as a degree of manifestation of amphimictic properties. Given the ambiguous role of the male gametophyte in the reproduction of *T. officinale*, we considered the functional state of pollen grains as some general diagnostic index reflecting its response to environmental heterogeneity. It is known that spatial heterogeneity of the environment is the key factor influencing the processes of plant adaptation.

When studying the functional state of the male gametophyte of *T. officinale*, we found that the proportion of fertile pollen grains in the plants growing within agrozems was higher than that on technozems, which may be associated with increased pollution of the latter with HMs. This is consistent with the published data that indicate a decrease in pollen quality in plants under the impact of technogenic factors (Tretjakova and Bagina, 2000; Tret'yakova and Noskova, 2004; Kisternyi and Panicheva, 2012; Korshikov et al., 2015).

In addition, it was found that the two forms of dandelions studied differ significantly in the proportion of fertile pollen grains and in the dependence of this index on environmental conditions. In *f. dahlstedtii*, the proportion of fertile pollen grains formed on the plant is lower than that in *f. pectinatiforme* and little changes in the gradients investigated. For example, in

the coenopopulations of sites A-1 and A-2, as well as T-1 and T-2, the differences between the index studied in this form were statistically nonsignificant. A slight increase in the proportion of fertile pollen grains in *f. dahlstedtii* was detected only in the plants growing on site T-3 (see Fig. 1). Possibly, the amphimictic properties, which ensure the necessary genetic heterogeneity of the coenopopulation, are enhanced in this form under the influence of adverse edaphic conditions (high HM contamination and agrochemical parameters of soils).

In *f. pectinatiforme*, plants from different coenopopulations growing on both agrozems and technozems differ more significantly in the proportion of fertile pollen grains (see Fig. 1). On these sites, the proportion of fertile pollen grains in this form increased in the coenotic competition gradient associated with the succession age (see A-1 → A-2 and T-2 → T-1). Under the most unfavorable edaphic conditions on site T-3, the proportion of fertile pollen grains was 10% lower compared to site T-1. However, the proportion of full-fledged seeds in the calathid in this gradient changed nonsignificantly (97.9 and 94.6%, respectively). This was probably due to the enhancement of apomictic properties in *f. pectinatiforme* under edaphic stress.

Statistical analysis showed significant differences between the morphological forms of *T. officinale* in the proportion of fertile pollen grains in the gradient of conditions studied (Table 2).

Thus, an increase in coenotic competition in the course of succession and unfavorable edaphic conditions lead to an increase in the intraspecific differentiation by the pollen fertility trait, which is probably due to a change in the way of reproduction in the morphological forms of dandelions studied. Under conditions of coenotic stress, the amphimictic properties sharply

increase only in *f. pectinatiforme*, due to which the benefits of sexual reproduction are realized. Under the conditions of edaphic stress, *f. pectinatiforme* enhances the apomictic properties, whereas *f. dahlstedtii* enhances the amphimictic properties, which allows realizing the advantages of both ways of reproduction. The adaptive value of the combination of amphimixis and apomixis has been shown for cereals (De Wet and Stalker, 1974; cited in Glazunova, 1983).

The viability of pollen grains is a more conserved index than their fertility.

Despite the fact that the data on the pollen grain viability were obtained under laboratory conditions at a certain sucrose concentration and temperature, it can be assumed that this index reflects the amphimictic properties, i.e., the ability of *Taraxacum officinale* to reproduce sexually under natural conditions.

On agrozem and technozem sites, the pollen grain viability is statistically independent of both the morphological form of dandelions and the combined effect of the form and site (see Table 3). The effect of the "site" factor was manifested significantly only when sites within each soil group differing in the level of coenotic competition and edaphic conditions were considered (Table 3). At a low level of coenotic competition, *T. officinale* behaves more like an apomict (the proportion of viable pollen grains is low), whereas under conditions of increasing coenotic competition for environmental resources, it demonstrates the ability to reproduce sexually (a higher ability to form pollen tubes). Amphimixis increases the heterogeneity of the offspring and, therefore, the competitiveness of the coenopopulation. However, in the gradient of coenotic competition, the proportion of viable pollen grains increases only to a certain level (not more than 20%). Apparently, this is a manifestation of the property of *T. officinale* as a facultative apomict.

The differences revealed in the proportion of viable pollen grains of the forms of dandelions studied growing in different sites within agrozems and technozems are statistically significant, whereas the differences between the pooled soil groups and the morphological forms of dandelions are nonsignificant. This allows considering the enhancement of the amphimictic properties in the gradient of coenotic competition as a general pattern. The data obtained in this study are consistent with the opinion of Maynard Smith (cited in Gilyarov, 1982), who believed that the initial stages of succession (open ecological niches) are more favorable for apomicts than for amphimicts.

CONCLUSIONS

(1) The pollen grain fertility is a characteristic of the male gametophyte more environmentally dependent in comparison with its viability. In general, the pollen fertility in dandelions growing on agrozems is

higher than that on technozems and differs in the two morphological forms studied.

(2) Under favorable conditions, the proportion of fertile pollen in *f. dahlstedtii* and *f. pectinatiforme* differs nonsignificantly. Under stress, the differences between the forms of dandelions in this index increase, which is possibly a mechanism of adaptation of the species to adverse environmental factors. Morphological forms, realizing two different reproductive strategies in stress, ensure the maintenance of abundance, on the one hand, and the genetic heterogeneity of coenopopulations, on the other hand.

(3) The proportion of viable pollen grains increases in the gradient of coenotic competition only to a certain level, which can be considered as a manifestation of the properties of a facultative apomict.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

REFERENCES

- Atabekova, A.I. and Ustinova, E.I., *Tsitologiya rasteniy* (Plant Cytology), Moscow: Agropromizdat, 1987.
- Bezel, V.S., Zhuikova, T.V., and Pozolotina, V.N., The structure of dandelion cenopopulations and specific features of heavy metal accumulation, *Russ. J. Ecol.*, 1998, vol. 29, no. 5, pp. 331–337.
- Calabrese, E.J., Hormesis: why it is important to toxicology and oxicologists, *Environ. Toxicol. Chem.*, 2008, vol. 27, no. 7, pp. 1451–1474.
<https://doi.org/10.1897/07-541>
- Cherepanov, S.K., *Sosudistye rasteniya Rossii i soprodel'nykh gosudarstv (v predelakh byvshego SSSR)* (Vascular Plants of Russia and Adjacent Countries (within the Area of the Former USSR), St. Petersburg: Mir i sem'ya, 1995.
- Elkarmi, A. and Eideh, R.A., Photosynthetic rates and antioxidant enzyme activity of *Platanus occidentalis* growing under two levels of air pollution along the streets of Seoul, *J. Plant Biol.*, 2006, vol. 49, no. 1, pp. 9–15.
<https://doi.org/10.1007/BF03031162>
- Ereschenko, O.V., The influence of environmental factors on the formation of birch (*Betula pendula* Roth.) pollen in urban ecosystems, *Izv. Alt. Gos. Univ.*, 2014, nos. 1–3, pp. 25–28.
- Ermakova, I.M., *Taraxacum officinale*: nomenclature and systematic position, in *Biologicheskaya flora Moskovskoi oblasti* (Biological Flora of Moscow Oblast), Pavlov, V.N., Rabotnov, T.M., and Tikhomirov, V.N., Eds., Moscow: Mosk. Univ., 1990, pp. 210–269.

- Flora SSSR (Flora of the USSR)*, Tsvelev, N.N., Ed., Moscow: Nauka, 1964, vol. 29.
- Foster, C.B. and Afonin, S.A., Abnormal pollen grains: an outcome of deteriorating atmospheric conditions around the Permian–Triassic boundary, *J. Geol. Soc.*, 2005, vol. 162, no. 4, pp. 653–659.
<https://doi.org/10.1144/0016-764904-047>
- Gilyarov, M.S., Ecological significance of parthenogenesis, *Usp. Sovrem. Biol.*, 1982, vol. 93, no. 1, pp. 10–22.
- Glazunova, K.P., Apomixis in East European representatives of the genus *Alchemilla* L., *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow, 1983.
- Hofsten, D.G., *Studier oder staket Taraxacum Wigg. med sarsstad hanvishing till Gruppen Vulgaris*, Stockholm, Dts Forl., 1954.
- Ivanov, A.I., Statsenko, A.P., Selina, E.E., and Skobaneva, O.V., Using pollen of woody and herbaceous plants as bioindicators of environmental pollution, *Vestn. Dal'nevost. Otd. Ross. Akad. Nauk*, 2009, no. 6, pp. 68–73.
- Ivshina, I.B., Kostina, L.V., Kamenskikh, T.N., Zhuiikova, V.A., Zhuiikova, T.V., and Bezel', V.S., Soil microbiocenosis as an indicator of stability of meadow communities in the environment polluted with heavy metals, *Russ. J. Ecol.*, 2014, vol. 45, no. 2, pp. 83–89.
- Kisternyi, G.A. and Panicheva, D.M., Vital capacity of *Pinus silvestris* from the plantations that are constantly under influence of alkaline and fluorine industrial emissions, *Vestn. Mosk. Gos. Univ. Lesa, Lesn. Vestn.*, 2012, no. 1 (84), pp. 145–147.
- Konchina, T.A. and Yashina, K.O., Expertise of urban school areas as regards to reaction of herbaceous plants pollen, *Molodoi Uchenyi*, 2015, no. 23, pp. 114–118.
- Korshikov, I.I., Lapteva, E.V., and Belonozhko, Yu.A., Quality of pollen and cytogenetic changes of scotch pine as indicators of the impact of the technogenically polluted environment of Krivoi Rog, *Contemp. Probl. Ecol.*, 2015, vol. 8, no. 2, pp. 250–255.
- Mirkin, B.M., Naumova, L.G., and Solomeshch, L.G., *Sovremennaya nauka o rastitel'nosti* (Contemporary Plant Science), Moscow: Logos, 2001.
- Pausheva, Z.P., *Praktikum po tsitologii rastenii* (Plant Cytology Tutorial), Moscow: Agropromizdat, 1988.
- Plisko, M.A., Embryological study of apomixis in Rosaceae and Compositae, in *Apomixis i selektsiya* (Apomixis and Selection), Moscow: Nauka, 1969, pp. 134–141.
- Poddubnaya-Arnoldi, V.A. and Dianova, V., Reproduction peculiarities of some rubber-bearing and non-rubber-bearing species of *Taraxacum* L., *Bot. Zh.*, 1937, vol. 22, no. 3, pp. 267–295.
- Pozolotina, V.N., Antonova, E.V., and Bezel, V.S., Comparison of remote consequences in *Taraxacum officinale* seed progeny collected in radioactively or chemically contaminated areas, *Ecotoxicology*, 2012, vol. 21, no. 7, pp. 1979–1988.
<https://doi.org/10.1007/s10646-012-0932-1>
- Pozolotina, V.N., Antonova, E.V., and Shimalina, N.S., Adaptation of greater plantain, *Plantago major* L., to long-term radiation and chemical exposure, *Russ. J. Ecol.*, 2016, vol. 47, no. 1, pp. 1–10.
- Rabotnov, T.A., *Taraxacum officinale* Wigg., in *Kormovye rasteniya senokosov i pastbishch SSSR* (Forage Herbs in Hayfields and Pastures in the USSR), Larin, I.V., Ed., Moscow: Sel'khozgiz, 1956, vol. 3, pp. 665–671.
- Rothmaler, W., Weitergefuehrt von H. Meusel und R. Schibert, in *Exkursionsflora fuer die Gebiete der DDR und der BRD*, Berlin: Volk und Wissen, 1972, pp. 254–279.
- Shimalina, N.S., Pozolotina, V.N., Orekhova, N.A., and Antonova, E.V., Assessment of biological effects in *Plantago major* L. seed progeny in the zone of impact from a copper smelter, *Russ. J. Ecol.*, 2017, vol. 48, no. 6, pp. 513–523.
- Shvartsman, P.Ya., *Polevaya praktika po genetike s osnovami selektsii* (Field Practice on Genetics with the Basics of Selective Breeding), Moscow: Prosveshchenie, 1986.
- Tretjakova, I.N. and Bagina, E.V., Structure of crown as well pollen and seed viability of fie (*Abies sibirica* Ledeb.) in disturbed forest ecosystems of the Khamar–Daban MTS near Baical Lake, *Ecologia* (Bratislava), 2000, vol. 19, pp. 280–294.
- Tretyakova, I.N. and Noskova, N.E., Pollen of *Pinus sylvestris* under conditions of ecological stress, *Russ. J. Ecol.*, 2004, no. 1, pp. 296–300.
- Tupitsyn, S.S., Ryabogina, N.E., and Tupitsyna, L.S., Level of teratogenesis as an indicator of the state of a biological object in different environmental conditions, *Izv. Samar. Nauchn. Tsentra Ross. Akad. Nauk*, 2012, vol. 14, nos. 1–3, pp. 822–828.
- Whittaker, R.H., *Communities and Ecosystems*, Macmillan, 1975.
- Zhuiikova, T.V., Severyukhina, V.S., Bezel, V.S., and Prushinskaya, N.M., Reaction of male gametophyte of *Taraxacum officinale* s. l. to chemical pollution of environment, *Contemp. Probl. Ecol.*, 2007, no. 3, pp. 511–516.
- Zhuiikova, T.V., Meling, E.V., Kaigorodova, S.Yu., Bezel', V.S., and Gordeeva, V.A., Specific features of soils and herbaceous plant communities in industrially polluted areas of the Middle Urals, *Russ. J. Ecol.*, 2015, vol. 46, no. 3, pp. 213–221.
- Zvereva, E.L., Lanta, V., and Kozlov, M.V., Effects of sap-feeding insect herbivores on growth and reproduction of woody plants: a meta-analysis of experimental studies, *Oecologia*, 2010, vol. 163, no. 4, pp. 949–960.
<https://doi.org/10.1007/s00442-010-1633-1>

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