

Diversity of photoperiodic responses in oats

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The article presents the results of an evaluation of the earliness and photoperiodic response (PPR) in the long-day oat accessions of various geographic origin. The material for this study were 139 oat accessions from the global collection of plant genetic resources maintained by the Vavilov Institute (VIR), which included landraces, breeding cultivars, and lines. In addition, the donors of low sensitivity to photoperiod developed at VIR were tested. A preliminary field study of the oat collection for early maturity and growing plants in the vegetation experiment was carried out according to the VIR Guidelines. The early accessions from VIR's oat collection identified in the field showed a great diversity of their photoperiodic responses during the vegetation experiment in a photoperiod facility. By origin, most of the accessions described in the vegetation experiment as earliness and weakly responsive to photoperiod were from Brazil (66 %); others from the USA, Portugal, Turkey, Colombia and Australia. Most of the Russian cultivars studied (77 %) were sensitive to a short photoperiod. Among donors with different photoperiodic responses, Skorospely 1 and Skorospely 2 were weakly responsive to photoperiod, while Srednespely 1 and Srednespely 2 showed medium responses. Many years of field studies and vegetation experiments with the oat genetic diversity from the VIR global collection have resulted in identifying genotypes characterized by earliness and weak photoperiodic responses. These accessions are of special value for breeders and currently being used to develop new early and productive oat cultivars.

Key words: oats; earliness; donors; photoperiodic sensitivity; photoperiod.

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Разнообразие фотопериодической чувствительности у овса

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В статье изложены результаты изучения скороспелости и фотопериодической чувствительности длиннодневной культуры овса различного географического происхождения. Материалом для исследования послужили 139 образцов овса из мировой коллекции генетических ресурсов растений Всероссийского института генетических ресурсов растений им. Н.И. Вавилова (ВИР), в том числе местные селекционные сорта и линии. Кроме того, в анализ были взяты доноры слабой чувствительности к фотопериоду, созданные в ВИР. Предварительное полевое исследование коллекции овса на скороспелость и выращивание растений в вегетационном опыте проводили по методикам ВИР. Изученные в полевых условиях скороспелые образцы коллекции овса ВИР показали большое разнообразие по чувствительности к фотопериоду в вегетационном опыте в фотопериодическом павильоне. Большинство образцов, охарактеризованных в вегетационном опыте как скороспелые и слабочувствительные к фотопериоду, происходят из Бразилии (66 %), также были образцы из США, Португалии, Турции, Колумбии и Австралии. Большая часть изученных российских сортов (77 %) оказалась чувствительной к короткому фотопериоду. Среди доноров с различной фотопериодической чувствительностью слабочувствительными к фотопериоду были Скороспелый 1 и Скороспелый 2, а среднечувствительными – Среднеспелый 1 и Среднеспелый 2. В результате многолетнего полевого и вегетационного изучения генетического разнообразия образцов из коллекции ВИР выделены генотипы со скороспелостью и слабой фотопериодической чувствительностью, представляющие особую селекционную ценность, которые в настоящее время вовлекаются в процесс создания новых скороспелых продуктивных сортов овса.

Ключевые слова: овес; скороспелость; доноры; фотопериодическая чувствительность; фотопериод.

Introduction

The most important factors affecting the duration of a plant's growing season, especially its first half, are the daylight length and the temperature regime. The research on photoperiodism, started in the early 20th century, made it possible to understand

and study in more detail mechanisms of the development of many crops (Garner, Allard, 1920, 1923; Gilbert, 1926).

Since the beginning of the 1920s, the effect of environmental factors on the growth and development of various plant species has been actively investigated. On N.I. Vavilov's initia-

tive, such research was conducted under the leadership of N.A. Maksimov, a well-known plant physiologist. Having analyzed literary sources and the intraspecific diversity of a number of crops, N.A. Maksimov (1929) made a conclusion about the effect of the daylight duration and temperature regime on the time between germination and flowering and the length of the whole growing season. N.I. Vavilov's geographic experiments (1928) confirmed the role of photoperiod in plant development. Afterwards, V.I. Razumov, Maksimov's disciple and follower, examining the intraspecific diversity of crops maintained in VIR's collection, identified plant species with strong and weak responses to daylength. He also noticed that their response to daylength was not always associated with their geographic origin and could be affected by definite growth conditions (Razumov, 1961).

By that time, it had been ascertained that a majority of cereal crops were long-day plants that needed a definite temperature regime, prolonged day and short night to reach the flowering phase (Wiggans, Frey, 1955). It was also shown that daylength and vernalization were two most important factors affecting the flowering process and, thereby, the yield formation (Sorrells, Simmons, 1992; Summerfield et al., 1997).

Some researchers have noted the effect of daylength on the passing of individual phases in oat development (Rodionova et al., 1994). Studying photoperiodic responses on a broad sample of common oat cultivars has helped to identify accessions highly responsive to the daylight duration and temperature regime as well as weakly responsive ones, the latter being recommended to breeders as sources of earliness (Merezhko, 1980; Rodionova et al., 1985; Merezhko, Ivanova, 1989; Ivanova et al., 1990; Koshkin et al., 2003, 2010).

For most of wild oat species, initial phases of their development have peculiarities in terms of their responses to environmental factors, including photoperiod and temperature (Paterson et al., 1976). A study of the ontogenesis of wild *Avena* L. species under long-day and short-day conditions showed that after 40 days of vernalization weak photoperiodic responses were typical for a number of accessions of diploid and tetraploid species, while various accessions of diploid, tetraploid and hexaploid oat species demonstrated a strong photoperiodic response (Loskutov, 2001). The most interesting among those accessions were early spring genotypes weakly responsive to daylength, originated from the Canary Islands (Spain), Corsica (France), Crete (Greece), Turkey, Tunisia, Lebanon and Ethiopia. All of them may potentially serve as source material for breeding early oat cultivars (Loskutov, 2007; Loskutov, Rines, 2011).

While studying cultivated oat species, a unique accession with a weak response to photoperiod was identified: a local cultivar from Turkey (CAV 2700) (Sampson, Burrows, 1972). On its basis a number of oat cultivars weakly responsive to photoperiod have been developed in Canada (Burrows, 1984, 1990, 1992). Low photoperiodic sensitivity was also described for accessions representing the endemic cultivated tetraploid species from Ethiopia *A. abyssinica* (Razumov, 1961; Arias, Frey, 1973).

For the *Dil* gene responsible for the effect of photoperiod in oats, two markers were identified using the RAPD analysis (Wight et al., 1994). Those molecular markers have been used to identify the dominant allele of *Dil* in oat breeding lines.

In Brazil, oat lines were studied using molecular markers (AFLP) associated with the flowering time; besides, their location on the genetic map was compared with other loci that may also affect the time of flowering. Those results were used for the development of oat breeding lines with an optimal set of alleles, providing earliness in the short-day environments of the southern hemisphere (Locatelli et al., 2006). The flowering time is an important factor in oat's adaptation to growth conditions. Genotypes differing in their responses to photoperiod and vernalization may prove useful when selecting parent pairs for the development of new cultivars, which would make use of the duration of the growing season with more efficiency (Locatelli et al., 2008). Some oat cultivars require low temperatures (vernalization) for flowering initiation. To analyze this factor, genes associated with oat vernalization were cloned in oat cultivars, and markers (QTL) connected with the response to vernalization were identified (Nava et al., 2012). In addition, the quantitative trait loci (QTL) controlling flowering periods in oats under varying durations of photoperiod and vernalization were mapped (Holland et al., 1997, 2002).

Analyzing responses to photoperiod and vernalization is of high practical importance, because these traits are closely linked with the growing season duration. At the same time, these factors may produce an effect on individual stages of plant development, especially on the durations of the periods between germination and booting and between germination and heading. It should be taken into account when definite accessions are used as source material for breeding (Koshkin et al., 2003, 2009, 2013).

The objective of this work has been to characterize a large number of accessions from the oat collection according to their photoperiodic responses and identify truly earliness source material with a weak response to photoperiod for further use in breeding programs in various regions of the Russian Federation.

Materials and methods

The experiments to assess photoperiodic responses were performed at the vegetation and photoperiod facilities of VIR's Department of Physiology on the grounds of Pushkin Laboratories of VIR in 2011–2018.

The material for the present research were 139 accessions of oats from the global collection of plant genetic resources held by the Vavilov Institute (VIR), which included landraces, breeding cultivars and lines from Russia, Ukraine, Norway, Slovakia, Germany, Turkey, Algeria, Portugal, Italy, China, Japan, Ethiopia, Canada, the USA, Mexico, Ecuador, Colombia, Peru, Brazil and Australia. The cultivar Privet (k-14787, Moscow Province) was used as the reference.

Also studied were the donors of low sensitivity to photoperiod developed on the basis of crosses between two references in the vegetation experiment: the Mexican cv. Chihuahua (k-12230, Mexico) with a weak response to photoperiod and the local cv. Anatolischer (k-14668, Turkey) with a strong response. The vegetation experiment under short-day conditions resulted in selecting early oat lines weakly responsive to photoperiod (k-15547, Skorospely 1, and k-15548, Skorospely 2), lines with medium photoperiodic response (k-15549, Srednospely 1, k-15550, Srednospely 2), and a late line with a strong

response to photoperiod (k-15551, Pozdnespely). The early cultivar Chihuahua (k-12230, Mexico) and the late cultivar Anatolischer (k-14668, Turkey) were used as the references for this vegetation experiment.

Preliminary field screening of the oat collection for earliness was performed using the VIR technique (Loskutov et al., 2012). In the vegetation experiment, the plants were grown according to the method described by V.A. Koshkin et al. (2013). Phenotypic description was made as follows: the date of heading was recorded for each plant after the emergence of a half of the panicle from the flag leaf sheath, the stems were labeled with paper tags, and the duration of the germination–heading period was calculated.

Photoperiodic response (PPR) was assessed according to the extent of heading delay under short day (SD) (T_2) compared with long day (LD) (T_1), and the PPR coefficient (C_{PPR}) was calculated using the formula $C_{PPR} = T_2/T_1$, where T_1 and T_2 are the durations of the germination–heading period (days) observed in oat plants, respectively grown under natural long-day (17–18 hrs) and short-day (12 hrs) conditions. Oat accessions delaying their heading under SD by 1–20 days versus LD and having $C_{PPR} = 1.00$ –1.30 were classified as weakly responsive to photoperiod (Koshkin et al., 1994). Accessions with $C_{PPR} > 1.75$ were attributed to the category of strongly responsive cultivars. Mean errors were measured according to B.A. Dospikhov (1979).

Results

According to the data of the preliminary field screening (2010–2017) in the environments of Pushkin Laboratories of VIR (Town of Pushkin), all accessions demonstrated shortened germination–heading and germination–ripening periods by 8–15 days in all years of study, compared with cv. Privet that served as the reference in the field experiment, but under short-day conditions in the photoperiod facility they showed considerable differences in their heading time.

During the analysis of oat accessions for their photoperiodic responses in the vegetation experiment, the references showed the following results: the early Mexican cultivar Chihuahua in all years of study demonstrated a delay in heading under SD versus LD by 8.1 (5.8–9.3) days, and $C_{PPR} = 1.21$ (1.17–1.26), while the late Turkish local cultivar Anatolischer had a delay in heading by 35.8 (28.3–49.5) days and $C_{PPR} = 1.79$ (1.61–2.23).

All accessions of various origin involved in our research demonstrated under LD earlier heading than under SD. The photoperiodic response coefficient (C_{PPR}) varied in the studied sample of oat accessions from 1.02 to 2.23, while the heading delay under SD versus LD averaged from 0.7 to 49.5 days (Table 1, Figs. 1, 2).

The results for many years of study showed that the following accessions were highly responsive to photoperiod: k-15357, GN 08207, k-15361, GN 09146, k-15361, GN 09146 (Norway), k-15369, St. Aleixo (Portugal), k-15226, MF 9521-462, k-15258, PA 7836-2701 (USA), k-12235, Desnuda (Peru), and k-15031, Portuguesa (Brazil).

Early accessions with weak responses to photoperiod, selected in the field experiment and identified during many years of the vegetation experiment, are presented in Table 2. Most of them originated from Brazil: these are cultivars (URS Corona, URS Guara, URS Penca, URS Guana, URS Charrua,

Table 1. Distribution of the studied oat accessions by country of origin (Pushkin, 2011–2018)

Origin	Number of accessions studied	Number of unresponsive accessions	Mean C_{PPR}	Dispersion of C_{PPR}
Russia	13	3	1.39	1.20–1.85
Norway	5	0	1.85	1.76–2.07
Portugal	2	1	1.56	1.23–1.88
Italy	1	0	1.38	1.38
Germany	1	0	1.46	1.46
Slovakia	1	0	1.73	1.73
Ukraine	1	0	1.31	1.31
Turkey	3	1	1.58	1.16–2.23
India	1	0	1.68	1.68
China	7	1	1.46	1.29–1.63
Japan	1	0	1.58	1.58
Algeria	1	0	1.57	1.57
Ethiopia	1	0	1.49	1.49
Canada	2	0	1.38	1.32–1.43
USA	25	6	1.48	1.07–1.94
Mexico	3	1	1.37	1.19–1.60
Ecuador	1	0	1.57	1.57
Peru	6	0	1.65	1.30–1.90
Colombia	1	1	1.24	1.21–1.27
Brazil	57	31	1.33	1.02–1.91
Australia	6	2	1.39	1.2–1.69

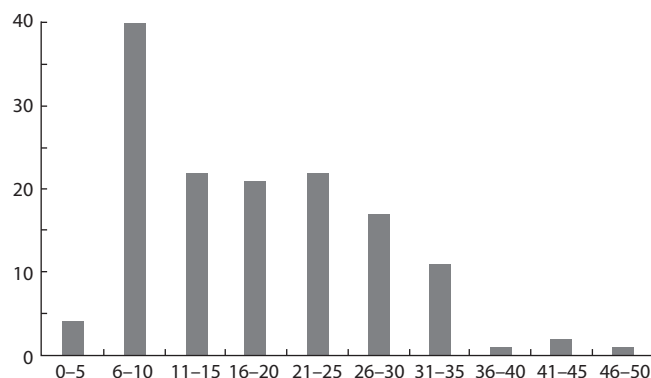


Fig. 1. Distribution of panicle delay with short daylight vs. long daylight in spring oat varieties studied (Pushkin, 2011–2018).

URS Guria, URS Brava, etc.) and breeding lines (UPF 77S090, UPF 798369-1-2, UFRGS1061503, UFRGS 20, UFRGS 077026-2, UFRGS 086004-1, etc.). Four accessions were from the United States: Common, breeding line C.I. 4627 from Mis-

Table 2. Characterization of oat accessions with weak response to photoperiod according to their PPR level (Pushkin, 2011–2018)

VIR catalog No.	Name	Origin	Germination to heading, days		T ₂ -T ₁	C _{PPR}
			T ₁	T ₂		
12230	Chihuahua, st.	Mexico	37.3±0.55	44.5±1.00	8.1	1.21
14668	Anatolischer, st.	Turkey	46.6±0.43	82.3±2.07	35.8	1.79
15316	Dast	Russia	33.6±0.16	43.5±0.82	9.9	1.29
15547	Skorospely 1	Russia	36.0±0.33	40.7±0.41	4.7	1.21
15548	Skorospely 2	Russia	33.9±0.10	40.8±0.47	6.9	1.27
15106	St. Romao	Portugal	39.1±0.38	48.1±0.11	9.0	1.23
7751	Local	Turkey	37.4±0.82	43.4±0.67	6.0	1.16
4403	Common	USA	32.1±0.23	34.5±0.73	2.4	1.07
12836	C.I. 4627	USA	34.8±0.55	41.5±0.68	6.7	1.19
15153	B 525-336	USA	38.8±0.61	48.5±0.68	9.7	1.25
15216	Pl. 629063	USA	38.7±0.26	48.6±0.52	9.9	1.26
15111	L-15	Columbia	37.8±0.40	45.8±0.52	8.7	1.24
14009	UPF 77S090	Brazil	37.1±0.23	43.2±0.32	6.1	1.16
14010	UPF 798369-1-2	Brazil	39.5±0.52	45.9±0.91	6.4	1.16
14011	UPF 477S030	Brazil	37.0±0.15	46.4±0.92	9.4	1.26
15481	URS Corona	Brazil	37.6±0.43	46.0±1.07	8.4	1.22
15482	URS Guara	Brazil	34.7±0.21	40.4±0.54	5.7	1.16
15483	URS Penca	Brazil	34.1±0.38	42.6±0.94	8.5	1.25
15484	URS Guana	Brazil	39.2±0.92	46.2±0.46	7.0	1.18
15485	URS Tarimba	Brazil	32.9±0.35	42.3±0.30	9.4	1.29
15486	URS Charrua	Brazil	34.8±0.33	39.9±0.62	5.1	1.15
15487	URS Guria	Brazil	38.4±0.52	46.1±0.69	7.7	1.20
15488	URS Toprena	Brazil	41.3±1.24	50.1±1.39	8.8	1.21
15490	URS Brava	Brazil	38.9±0.39	47.4±0.78	8.5	1.22
15491	URS Estampa	Brazil	38.7±0.30	48.6±0.60	9.9	1.26
15492	UFRGS 017129-1	Brazil	35.1±0.67	43.4±0.82	8.3	1.24
15493	UFRGS1061503	Brazil	38.3±0.62	43.9±0.88	5.6	1.15
15533	UFRGS 8	Brazil	43.0±0.26	52.7±0.91	9.7	1.23
15534	UFRGS 9	Brazil	37.5±0.34	46.8±1.06	9.3	1.25
15541	UFRGS 17	Brazil	44.5±0.58	52.9±0.59	8.4	1.19
15543	UFRGS 19	Brazil	47.3±1.71	51.4±1.16	4.1	1.09
15544	UFRGS 20	Brazil	36.1±0.28	42.9±0.35	6.8	1.19
15546	UFRGS 22	Brazil	36.6±0.60	46.0±1.42	9.4	1.26
15598	UFRGS 077026-2	Brazil	39.2±1.36	44.5±0.37	5.3	1.14
15600	UFRGS 086208-3	Brazil	33.6±0.45	43.1±1.21	9.5	1.28
15609	UFRGS 953195	Brazil	36.2±1.23	44.1±0.59	7.9	1.22

Table 2. (End)

VIR catalog No.	Name	Origin	Germination to heading, days		T ₂ -T ₁	C _{PPR}
			T ₁	T ₂		
15678	UFRGS 086004-1	Brazil	35.6 ± 1.12	42.1 ± 0.87	6.5	1.18
15681	UFRGS 086092-2	Brazil	35.4 ± 1.30	42.6 ± 1.41	7.2	1.20
15682	UFRGS 086136-5	Brazil	40.3 ± 2.05	41.0 ± 0.62	0.7	1.02
15683	UFRGS 086183-2	Brazil	33.4 ± 0.38	41.6 ± 0.58	8.2	1.25
8271	Gidgee	Australia	31.3 ± 0.30	37.6 ± 0.43	6.3	1.20
15173	Mitika	Australia	38.4 ± 0.68	46.4 ± 0.40	8.0	1.21

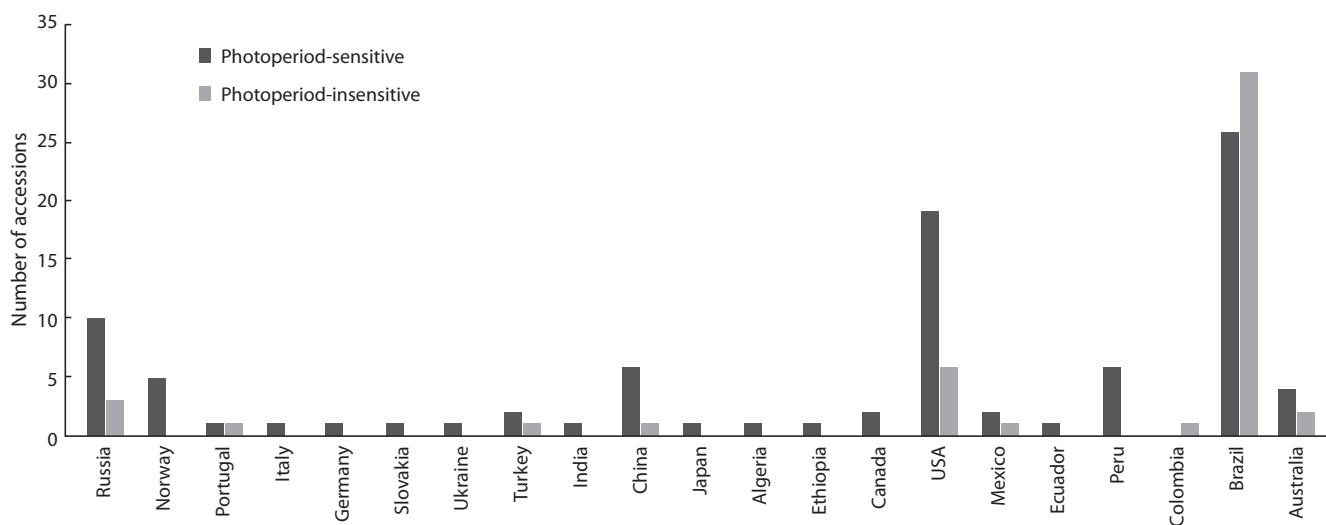


Fig. 2. Sensitive and insensitive oat accessions with regard to their geographic origin (Pushkin, 2011–2018).

Table 3. Characterization of oat donors with various photoperiodic responses according to their C_{PPR} (Pushkin, 2016–2018)

VIR catalog No.	Name	Origin	Germination to heading, days		T ₂ -T ₁	C _{PPR}
			T ₁	T ₂		
12230	Chihuahua, st.	Mexico	37.3 ± 0.55	44.5 ± 1.00	8.1	1.21
14668	Anatolischer, st.	Turkey	46.6 ± 0.43	82.3 ± 2.07	35.8	1.79
15547	Skorospely 1	Russia	37.8 ± 0.58	46.5 ± 0.87	8.4	1.22
15548	Skorospely 2	Russia	34.9 ± 0.45	48.3 ± 0.85	11.3	1.30
15549	Srednospely 1	Russia	39.4 ± 0.37	57.6 ± 0.68	14.7	1.46
15550	Srednospely 2	Russia	36.2 ± 0.39	65.3 ± 1.77	22.9	1.56
15551	Pozdnospely	Russia	40.1 ± 0.53	64.9 ± 0.72	26.9	1.65

souri, etc., and the other accessions originated from Portugal, Turkey, Colombia and Australia.

Most of the accessions characterized in the vegetation experiment as early and weakly responsive to photoperiod came from Brazil (66 %). A majority of the tested Russian cultivars (77 %) appeared responsive to short-day photoperiod.

In addition to the accessions from the oat collection, in 2016–2018 a set of donors with various photoperiodic responses were examined (Table 3): two lines weakly responsive to photoperiod, Skorospely 1 and Skorospely 2, which had on average a minor delay under SD (8.4 and 11.3) versus LD and low C_{PPR} = 1.22, 1.30, whereas lines with medium response to

photoperiod, Srednespely 1 and Srednespely 2, considerably delayed their development under short-day conditions and had higher $C_{PPR} = 1.46$ and 1.56 . The highest $C_{PPR} = 1.65$ was observed in the late line Pozdnespely.

Conclusion

Early oat accessions from the VIR global collection, screened in the field, showed greater diversity in their responses to photoperiod when tested in the vegetation experiment in the photoperiod facility. The early cultivars with weak responses to photoperiod, identified in the course of the present study, and the developed donors are of special importance for breeders, and are presently being involved in breeding programs in order to develop new earliness and high-yielding oat cultivars.

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