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Influence of vernalization and photoperiod to the vegetation period of wild species of oats (*Avena* spp.)

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Summary

This paper presents the results of a six year field study of wild *Avena* species and their response to vernalization and photoperiod. The accessions of twenty one wild and weedy species were tested under 12-hr and 18-hr daylength and cold temperatures (for 40 days at +2 °C) treatments and without it (as a control). The results demonstrate that for the majority of species evaluated, cold temperature requirements had a greater influence on heading date and the duration of the vegetative period than daylength. Genotypes with neutral, weak and strong reactions to all treatments were found and spring and winter types were selected. The results further demonstrated that daylength-insensitive forms occurred in the south Mediterranean region and adjacent southern territories.

Introduction

Response to daylength and vernalization are two of the most important mechanism controlling flowering, and therefore yield, in many of our crop plants (Gilbert, 1926). Photoperiodism and vernalization responses, are controlled by many genes (Ppd, Vrn, etc.), and in some cases, cold temperatures and or short days are a pre-requisite to response to long days (Kirby, 1969; Sorrells & Simmons, 1992; Summerfield et al., 1997). Individual genes which have qualitative effects on these responses have been identified using high molecular markers (Holland et al., 1997; Wight et al., 1994).

Centres of origin and diversity of wild and weedy relatives of oat are clustered in the Mediterranean region, the countries on the coasts of the Black and Caspian Seas and the countries of Central Asia. The richest diversity appears to be between latitudes 30° to 40°N (Baum, 1977). The first vegetative phase of many wild oat species takes place during the cold months and those which grow at high elevations (2000 m) have specific responses to the photoperiod and cold temperatures imposed by environmental conditions at these altitudes (Darmency & Aujas, 1986; Paterson et al., 1976). There are strong interrelationships during the early stages of plant ontogenesis, (germination-tillering-heading) and it is very important to take this into account when using certain wild weedy species as the initial material in breeding programmes. Vernalization and long day requirements in *Avena* are quantitative rather than obligatory, and during these studies, a unique daylength insensitive accession CW 544 (CAV 2700) which originated from Turkey was identified and subsequently used to develop novel oat cultivars (Burrows, 1986; Sampson & Burrows, 1972).

The influence of daylength and the effect of lower temperatures during early plant development in spring (Bleken & Skjelvag, 1986; Doroshenko & Razumov, 1929; Hellewell et al., 1996; King & Bacon, 1992; Razumov, 1961; Shands & Cisar, 1982; Wiggans & Frey, 1955), and winter (Qualset & Peterson, 1978; Thomas & Naqvi, 1991) has been observed by many researchers in oat cultivars and species.

The present research was prompted by three practical considerations: 1) To establish whether daylength or cold requirements has the greatest influence on heading date of the wild oat species studied here under the environmental conditions prevalent in St. Petersburg at a latitude of 60°N. 2) To identify accessions

Table 1. Late-ripening accessions of oat species, which were evaluated in vegetation experiments (1991–1996)

Species	Origin	Ploidy	Number of evaluated accessions	Percent of evaluated accessions from species collection (%)
A. bruhnsiana	Azerbaijan	2	1	50
A. ventricosa	Cyprus	2	1	50
A. clauda	Azerbaijan, Iran, Turkey	2	7	54
A. pilosa	Azerbaijan, Syria	2	4	15
A. longiglumis	Morocco, Israel	2	2	22
A. damascena	Syria	2	1	50
A. prostrata	Spain	2	1	50
A. canariensis	Spain (Canary is.)	2	2	33
A. wiestii	Azerbaijan, Israel	2	5	29
A. hirtula	Greece (Crete)	2	2	33
A. atlantica	Morocco	2	1	50
A. barbata	Azerbaijan, Portugal, France (Corsica), Italy, Greece (Pelopones), Turkey	4	8	10
A. vaviloviana	Ethiopia	4	3	6
A. agadiriana	Morocco	4	1	50
A. magna	Morocco	4	2	15
A. murphyi	Morocco	4	1	50
A. macrostachya	Algeria	4	1	50
A. ludoviciana	Azerbaijan, Russia, Ukraine	6	8	<1
A. sterilis	Russia, Georgia, Spain, Morocco, Tunisia, Lebanon, Kenya	6	9	<1
A. fatua	Azerbaijan, Tajikistan	6	2	<1
A. occidentalis	Spain (Canary is.)	6	6	45

insensitive to photoperiod and vernalization for subsequent utilisation in breeding programmes. 3) To establish if there is a relationship between geographical origin of the accessions studied and their sensitivity to photoperiod. This paper reports the findings of these considerations and relates them to breeding strategies.

Materials and methods

Approximately 1000 accessions of 21 wild species of oats (Rodionova et al., 1994) from diverse eco-geographical regions were evaluated for morphological characters and agronomic traits from 1990–1995 at the Pavlovsk Experimental Station of the Vavilov Institute of Plant Industry (VIR), St. Petersburg. The research was based on the International Descriptors List of *Avena* L. (1984). Most of the accessions studied were originally collected from regions considered to be centres of diversity of the genus and are listed in Table 1.

The vegetative evaluations were performed not on random accessions without any analysis of their characters, but representing the species diversity was selected on carefully. Under field conditions during several years about 70 late-ripening (vegetation period more than 120–130 days) samples were identified in all the species under study (Loskutov, 1993a, 1993b, 1998). All these accessions belonging to eleven diploid species, five tetraploid species and four hexaploid species are shown in Table 1. Several species which had late-heading accessions, especially in years (1991, 1993, 1995) with warm spring were used in this research.

Table 2. The mean duration of germination-heading period under different condition of vernalization and daylength (1991–1996)

Species	Duration, days			
	Without vernalization		Vernalization	
	LD (18-hr)	SD (12-hr)	LD (18-hr)	SD (12-hr)
A. bruhnsiana	48	–*	47	105
A. ventricosa	96	>150	47	–
A. clauda	>111	>156	42	>84
A. pilosa	>109	140	48	40
A. longiglumis	>97	140	37	44
A. damascena	>150	–	37	–
A. prostrata	95	–	36	–
A. canariensis	48	60	33	–
A. wiestii	82	101	44	59
A. hirtula	46	57	38	51
A. atlantica	69	113	54	–
A. barbata	99	117	47	69
A. vaviloviana	60	66	42	58
A. agadiriana	70	–	29	–
A. magna	49	>100	37	55
A. murphyi	111	>200	44	109
A. macrostachya	–	–	50	120
A. ludoviciana	>125	>183	47	88
A. sterilis	>97	>140	45	73
A. fatua	55	>120	47	>120
A. occidentalis	69	87	49	65

* The plants were very weak or germination was very low.

The vegetation experiment was conducted between 1991 and 1996 and a special site was constructed using lightproof shelters, so that the duration of photoperiod could be artificially reduced to 12 hour short days (SD). Natural daylength (Leningrad Province latitude 60°N) was used as the long day (LD) control, where average daylength in the period from germination to heading equalled 18 hours and the monthly deviations were of 18, 19 and 17 hours in late May, June and July respectively. For the cold treatments, seeds were vernalized for 40 days at +2 °C. The time interval from germination to heading was taken as the main criterion for evaluating the response of the species to daylength and to vernalization (yarovization). Differences between the variations in the time of heading during SD and LD treatments determined the degree of photoperiodic sensitivity of each accession (Loskutov & Ivanova, 1996).

A coefficient (C_{phot}) of photoperiodic sensitivity was calculated using the formula: $C_{phot} = T_2/T_1$, where T_1 is duration from germination-heading during LD and T_2 is duration from germination-heading during SD (Koshkin et al., 1994). With regard to vernalization response, a similar coefficient (C_{vern}) was calculated as follows: $C_{vern} = T_2/T_1$, where T_1 is duration from germination-heading after vernalization treatment and T_2 is duration from germination-heading without vernalization.

Results and discussion

The results demonstrated that many of the accessions studied did not head at all during the duration of the experiments, or that heading was delayed to such an extent that there was a considerable degree of sterility and deterioration of germination and seed quality. Classification of the late-heading accessions expressed as a percentage of the total experimental set is shown in Table 1.

The majority of the samples in most species sown with non-vernalized seeds were late ripening, and the duration of the period from germination to heading under natural LD fluctuated from 80 to 120 days. The LD treatment also led to a weak response to vernalization (less than 20 days delay in heading) in the following species: diploids – *A. bruhnsiana, A. hirtula, A. canariensis, A. atlantica,* tetraploids – *A. vaviloviana, A. magna*; hexaploids – *A. fatua* and *A. occidentalis*. Strong responses to vernalization (more than 20 days of delay in heading) were recorded in the following: diploids **–** *A. ventricosa, A. clauda, A. pilosa, A. damascena, A. postrata, A. longiglumis, A. wiestii*; tetraploids – *A. agadiriana, A. barbata, A. murphyi*; hexaploids *A. ludoviciana* and *A. sterilis* (Table 2). Several accessions were unable to proceed to reproductive development without vernalization. These true winter types were: diploids – *A. clauda* (WIR-200, WIR-269) from Azerbaijan and (WIR-1860) from Iran, *A. pilosa* (WIR-197), (WIR-207) from Azerbaijan, *A. longiglumis* (WIR-1874) from Morocco, and *A. damascena* (WIR-1862) from Syria; tetraploid – *A. barbata* (WIR-1758) from Portugal; hexaploids – *A. sterilis* (WIR-328) from Georgia (Abkhazia), and (WIR-283, WIR-326) from Russia (Krasnodar region), *A. ludoviciana* (WIR-350, WIR-383) from Ukraine (Crimea) and (WIR-323, WIR-384) from Russia (Krasnodar region). The latest forms of the tetraploid *A. vaviloviana* from Ethiopia which were vernalized and grown in LD conditions accelerated heading by 3–19 days. All accessions of the hexaploid *A. fatua* showed the weakest response to cold vernalization, although two relatively late samples of this species from Tadjikistan (Gorno-Badakhshan) and Azerbaijan (Nakhichevan), which were collected at altitudes of 2700 meters and 1050 meters above sea level respectively, exhibited an acceleration in heading date of only 4–10 days.

All the species studied, except *A. bruhnsiana, A. hirtula, A. magna* and *A. fatua*, exhibited accelerated heading under SD (12-hr) vernalization compare with the LD (18-hr) treatment without vernalization. Under the short-day vernalization treatment, these species showed the opposite response.

Studying the development of individual plants of wild species of genus *Avena* during ontogenesis in LD and SD conditions showed that after 40 days vernalization, weak photoperiodic sensitivity was typical for accessions of diploid species *A. wiestii, A. hirtula, A. longiglumis* and *A. canariensis*; tetraploid *A. vaviloviana*. Tetraploid *A. barbata* and hexaploid *A. occidentalis* were moderately sensitive to the treatments.

Strong photoperiodic sensitivity without vernalization was shown by the diploid species *A. bruhnsiana*, *A. ventricosa*, *A. clauda*, *A. pilosa*, *A. atlantica* and *A. longiglumis* and the tetraploids *A. magna*, and *A. murphyi* and the hexaploids *A. fatua, A. sterilis* and *A. ludoviciana* whose heading dates were delayed by 30–70 days in comparison to the LD treatment. The perennial autotetraploid *A. macrostachya* exhibited very strong photoperiodic sensitivity under cold vernalization and *A. magna* appeared to be a very daylength-sensitive species which agrees with the findings of Sampson & Burrows (1972).

Analysis of the response to vernalization treatments (less than 20 days delay in heading) of the different species identified several genotypes: diploid – *A. pilosa* (WIR-1890) from Syria, *A. hirtula* (WIR-1849) from Greece (Crete), *A. wiestii* (WIR-215, WIR-217) from Azerbaijan; tetraploids *A. barbata* (WIR-211) from Azerbaijan and (WIR-1848) from France (Corsica), *A. vaviloviana* (all accessions from Ethiopia) and hexaploid *A. sterilis* (WIR-1746) from Spain, (WIR-871) from Tunisia and (WIR-888) from Morocco, which demonstrated weak sensitivity to the change of daylight duration. Only one accession of *A. barbata* (WIR-805) from Turkey showed insensitivity to the change of photoperiod. The response of the Ethiopian endemic species *A. vaviloviana* which is very closely related to another Ethiopian species *A. abyssinica* Hoch. was described as an insensitive species by Razumov (1961).

Early flowering types heading from the 30th to 37th day after 40 days of cold temperatures were identified the accessions *A. clauda* (WIR-1907) from Turkey, *A. longiglumis* (WIR-1912) from Israel, *A. canariensis* (WIR-292, WIR-1917) from Spain (Canary, Fuerteventura), *A. prostrata* (WIR-1891) from Spain, *A. vaviloviana* (WIR-755) from Ethiopia, *A. agadiriana* (WIR-1895) and *A. magna* (WIR-1786) from Morocco and *A. ludoviciana* (WIR-953) from Azerbaijan. *A. wiestii* from Azerbaijan, and *A. vaviloviana* from Ethiopia displayed the weakest sensitivity to daylight duration. The latest heading accessions, *A. barbata* (WIR-1758) from Portugal, (WIR-1770) from Greece (Pelopones), *A. fatua* (WIR-337) from Tadjikistan (Gornyi-Badakhshan), (WIR-968) from Azerbaijan (Nakhichevan), *A. ludoviciana* (WIR-350, WIR-383) from Ukraine (Crimea) and (WIR-384) from Russia (Krasnodar region) were characterised by strong photoperiodic sensitivity and they failed to enter reproductive development in the SD experiment (12 hours of daylight without vernalization).

Table 3. The values of the coefficients C_{phot} and C_{vern} in oat species

Species	Ploidy	Coefficient C_{vern}	Coefficient C_{phot}
A. bruhnsiana	2	1.00	–
A. ventricosa	2	2.04	1.56
A. clauda	2	2.64	1.40
A. pilosa	2	2.27	1.40
A. longiglumis	2	2.62	1.44
A. damascena	2	4.05	–
A. prostrata	2	2.64	–
A. canariensis	2	1.45	1.25
A. wiestii	2	1.86	1.23
A. hirtula	2	1.20	1.24
A. atlantica	2	1.28	1.64
A. barbata	4	2.10	1.18
A. vaviloviana	4	1.42	1.10
A. agadiriana	4	2.40	–
A. magna	4	1.32	2.04
A. murphyi	4	2.52	1.80
A. macrostachya	4	–	2.40
A. ludoviciana	6	2.66	1.46
A. sterilis	6	2.15	1.44
A. fatua	6	1.17	2.18
A. occidentalis	6	1.41	1.26

To make results from the experiments more comparable the coefficients (C_{vern} and C_{phot}) were calculated (Table 3). The coefficient of response to vernalization (C_{vern}) demonstrated that *A. bruhnsiana* and *A. fatua* exhibited a neutral or weak response to vernalization; whilst *A. ventricosa, A. clauda, A. pilosa, A. damascena, A. longiglumis, A. atlantica, A. prostrata, A. agadiriana, A. barbata, A. ludoviciana* and *A. sterilis* showed a very strong response to cold temperatures. In most cases the influence of vernalization under SD was less than the coefficient of vernalization under LD. The coefficient of photoperiodic sensitivity (C_{phot}) demonstrates that *A. canariensis, A. wiestii* and *A. occidentalis* had a neutral or weak sensitivity to photoperiod whilst *A. magna* and *A. fatua* had a very strong sensitivity to daylength. In most cases the influence of cold pre-treatment under the two daylights gave a higher coefficient than plants which were not cold treated. *A. hirtula* and *A. vaviloviana* appeared to be particularly insensitive to any of the treatments and conversely, *A. murphyi* was demonstrably sensitive to both vernalization and photoperiod.

The response to both photoperiod and cold treatments of the various species and accessions in relation to their geographical origins are shown in Table 4. At all ploidy levels, most of the winter types originated from countries with a latitude north of 40°N. With the exception of accessions from Azerbaijan, all the accessions from these northerly latitudes showed a high level of daylength sensitivity. Azerbaijanian forms were very diverse in terms of daylength sensitivity, especially those from the regions of the Apsheron peninsula and the Lenkoran lowlands. True spring tunes from Nakhichevan (Azerbaijan) and Tadjikistan were very daylength-sensitive, whilst true winter types from other regions of Azerbaijan had pronounced daylength-sensitivity.

Spring and winter types from Morocco (latitude south of 40°N) displayed variable responses to photoperiod from weak to strong, whilst entries from Syria, Israel and Kenya were daylength insensitive or only moderately sensitive. The most interesting group were the true spring accessions of various ploidy levels which were daylength insensitive or had only very low levels of sensitivity, and who's origins were the Canary islands, Corsica, Tunisia, Lebanon, Crete, Turkey and Ethiopia.

Conclusion

The diversity in response to photoperiod and vernalization demonstrated by the results described here, illustrate the level of polymorphism for these characters within the wild genepool of the genus *Avena*. The diploid species were shown to be the most diverse group, 20–50% being late ripening, whilst true winter types which showed strong responses to the effect of vernalization were identified in some accessions of *A. clauda, A. barbata, A. ludoviciana* and *A. sterilis*. These accessions originated either from high altitudes or from regions where initial vegetative growth occurs during the winter months. *A. vaviloviana* and *A. fatua* may be regarded as true spring entries since only 6% and 1% of their total accessions respectively, manifested neutral or only a weak response to vernalization. Such insensitivity and very strong daylength-sensitivity illustrates the true spring nature of *A. fatua* which is a common, noxious weed of crop plants world-wide.

The diploids *A. wiestii, A. canariensis* and tetraploid *A. magna* appeared to be true spring types, and of the two latter species, only two accessions were

Table 4. Geographical aspects of oat species reaction to vernalization and photoperiod

Origin	Latitude	Vernalization response					Photoperiod response				
		neutral	weak	middle	strong	very strong	neutral	weak	middle	strong	very strong
Georgia	42				+			+			
Italy	44				+				+		
Greece (Pelopones)	38				+				+		
Portugal	40				+					+	
Cyprus	35				+					+	
Ukraine	45				+	+				+	
Russia	44				+	+				+	+
Iran	38				+	+					+
Spain	40				+						+
Azerbaijan:	41	+	+	+	+	+	+	+	+	+	+
– Apsheron peninsula		+	+	+	+	+	+	+	+	+	
– Lenkoran lowland				+				+	+		
– Nagornyi Karabakh				+				+			
– Nakhichevan		+									+
– Remained regions				+	+	+				+	
Syria	35			+		+		+			
Algeria	35								+		
Morocco	32		+	+	+	+		+	+	+	+
Tadjikistan	38		+								
Kenya	4			+						+	
Israel	32			+					+		
Greece (Crete)	35		+					+			
Tunisia	34		+					+			
Ethiopia	10		+					+			
Lebanon	34			+				+			
France (Corsica)	41			+				+			
Spain (Canary is.)	29		+	+			+	+			
Turkey	39			+			+	+			

demonstrably late flowering. *A. hirtula*, *A. vaviloviana* and *A. occidentalis* were neutral to photoperiod whilst *A. clauda*, *A. murphyi* and *A. sterilis* were late ripening with very strong daylength-sensitivity.

The results of this study have demonstrated that for the majority of wild species evaluated, cold requirements have more influence on heading date and the duration of the vegetative period than daylength. It has also been shown that the response of wild *Avena* species to cold temperature vernalization is to some extent linked with the geographic distribution of the accession and the response to daylength is species dependent. No strict correlation between species, their geographical origins and response to photoperiod was observed although several daylength-insensitive forms of various species originated from latitudes south of 40°N.

Finally, the results demonstrate that there is considerable eco-geographical and genetic variation in response to vernalization within the genus *Avena*, which, with careful selection of suitable accessions, will enable breeders to utilise the appropriate material for their agricultural environment.

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