

Variability of the photoperiod response in guar (*Cyamopsis tetragonoloba* (L.) Taub.) genotypes of different geographic origin

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The introduction of the new legume crop guar is of great practical importance for Russia, since it serves as a source of valuable vegetable raw material, guar gum, used for the food, gas and oil industry. The main problem with guar cultivation in the southern regions of the Russian Federation is that this plant should be grown under a short photoperiod. Prolonged daylight exposure is an obstacle to the timely transition of guar to flowering, which dramatically affects its productivity. In the study, 192 guar genotypes from the VIR collection were tested for the speed of transition to flowering on an extremely long photoperiod (18.2–18.9 h) in the greenhouse of the Pushkin experimental station of VIR (St. Petersburg). At the same time, the earliness of maturation of the same genotypes was estimated under the field conditions in the Kuban experimental station of VIR (Krasnodar area). Among the samples tested, genotypes with weak photoperiodic sensitivity (which were also early matured under the conditions of Krasnodar), as well as the highly photoperiod-sensitive genotypes were identified. It has been established that for the same guar plant the critical photoperiod initiating the formation of buds may not coincide with the critical photoperiod required for their flushing (i. e. flowering *per se*). The observed fact confirms the hypothesis reported earlier about a two-stage launch of the flowering program in guar, according to which budding and flowering itself are controlled by independent gene systems. According to our results, the successful breeding of early mature guar varieties ultimately depends on the first gene system that controls the initiation of budding in response to a critical photoperiod. We suggest that another hypothetical gene system can influence the dates of guar flowering, which determines the speed of vegetative development of a specific genotype, measured as the number of days from germination to the appearance of the first true leaf. Thus, sensitivity to photoperiod in guar is only one of several factors that determine the speed of a plant's transition to flowering, and it should not be assessed on the basis of the length of the period from germination to flowering, which is common in breeding practice. The results of the study show that, although the photoperiod sensitivity of guar limits the range of geographic latitudes in which the legume crop can be successfully grown, there is a real opportunity to overcome this limitation by selecting and propagating photoperiod-insensitive genotypes from the enormous genetic diversity of this species.

Key words: *Cyamopsis tetragonoloba* (L.) Taub.; guar; photoperiod; bud formation; initiation of flowering.

For citation: Teplyakova S.B., Volkov V.A., Dzyubenko E.A., Potokina E.K. Variability of the photoperiod response in guar (*Cyamopsis tetragonoloba* (L.) Taub.) genotypes of different geographic origin. Vavilovskii Zhurnal Genetiki i Selektzii = Vavilov Journal of Genetics and Breeding. 2019;23(6):730-737. DOI 10.18699/VJ19.547

Амплитуда изменчивости фотопериодической реакции генотипов гуара (*Cyamopsis tetragonoloba* (L.) Taub.) разного географического происхождения

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Интродукция новой бобовой культуры гуар на территорию Российской Федерации имеет большое практическое значение, так как обеспечивает импортозамещение гуаровой камеди – растительного сырья, используемого для целей пищевой, газо- и нефтедобывающей промышленности. Основная проблема при возделывании гуара в южных регионах РФ – потребность культуры в коротком фотопериоде. Увеличенная продолжительность светового дня препятствует своевременному переходу гуара к цветению, что резко сказывается на его продуктивности. В проведенном исследовании 192 генотипа гуара из коллекции ВИР испытывались на скорость перехода к цветению на экстремально длинном для культуры гуара фотопериоде (18.2–18.9 ч) в условиях теплицы Пушкинского филиала ВИР (Санкт-Петербург). Параллельно оценивалась

скороспелость этих же генотипов в условиях поля Кубанского филиала ВИР (Краснодарский край). Среди испытуемой выборки были выявлены как генотипы со слабой фотопериодической чувствительностью (они же и более скороспелые в условиях Краснодарского края), так и сильно чувствительные к фотопериоду. Установлено, что у одного и того же растения гуара пороговый фотопериод, инициирующий образование бутонов, может не совпадать с критическим фотопериодом, необходимым для их распускания (собственно цветения). Наблюдаемый факт подтверждает выдвинутую ранее гипотезу о двуступенчатом запуске программы цветения у гуара, согласно которой бутонизация и собственно цветение контролируются независимыми генными системами. По результатам экспериментов, в успешной селекции гуара на скороспелость решающую роль играет именно первая генная система, контролирующая запуск бутонизации в ответ на критический фотопериод. На отсрочку даты начала цветения у гуара может влиять еще одна гипотетическая генная система, которая определяет скорость вегетативного развития конкретного генотипа, измеряемую как количество дней от всходов до появления первого настоящего листа, и не зависит от фотопериода. Таким образом, фотопериодическая чувствительность у гуара является лишь одним из факторов, определяющих скорость перехода растения к цветению, и ее не следует оценивать по признаку «всходы–цветение», распространенному в растениеводческой практике. Результаты проведенного исследования показывают, что, хотя фотопериодическая чувствительность гуара ограничивает диапазон географических широт, в котором эта культура может успешно выращиваться, есть реальная возможность преодолеть указанное ограничение, отбирая и размножая соответствующие генотипы из имеющегося огромного генетического разнообразия культуры.

Ключевые слова: *Cyamopsis tetragonoloba* (L.) Taub.; гуар; фотопериодическая чувствительность; сроки бутонизации; сроки цветения.

Introduction

Guar (*Cyamopsis tetragonoloba* (L.) Taub.) is an annual legume plant, traditionally cultivated in India and Pakistan as a fodder and vegetable crop, and also used as a green fertilizer (Kuravadi et al., 2012). The increased attention to guar all over the world in recent years is due to the high content of galactomannan polysaccharide reserved in guar seeds. Galactomannans quickly hydrate in cold water at low concentrations, forming a viscous colloidal solution – guar gum, which is used as a thickener and stabilizer in the food, textile, gas and oil industries. It was reported that various sectors of the Russian economy demand each year at least 15 thousand tons of guar gum, which is currently being covered exclusively by imports. Thus, the introduction of guar as the new legume crop to the southern regions of Russian Federation and breeding of new guar varieties adapted to new ecological conditions is a relevant and popular topic (Startsev et al., 2017).

Although the ecological optimum of guar perfectly matches to the conditions of the semi-arid climatic zone of the north-west of India (~27° N), several attempts have been made to introduce this crop into higher latitudes: in the southern states of the USA – Texas (~29° N), Arizona (~34° N), Oklahoma (~35° N) (Lubbers, 1987), in southern Italy (~39° N) (Gresta et al., 2018). The main complication for successful guar cultivation in the countries of the higher latitudes is the prolonged vegetation period of plants causing harvesting delay before the onset of autumn rains, which negatively affects the yield. For example, the comparative study of the length of the vegetation of 68 guar genotypes of different geographical origin (India, Pakistan, USA, Australia) in conditions of southern Italy showed that this trait ranged from 155–163 days for the earliest maturing varieties, up to 175–184 days for the late-maturing genotypes. Under these conditions, the guar plants completed their vegetation from mid-October to early November. Therefore, it was concluded that early maturity is a key breeding trait for this crop when cultivated in the Mediterranean region (Gresta et al., 2018).

The length of vegetation period and, consequently, maturation rate, is predominantly determined by the photoperiodic sensitivity (PPS) of a plant. Guar is a short-day plant (Lubbers, 1987). The length of the daylight during the growing season in Jodhpur province (India), where this crop is widely cultivated, varies from 12.7 to 13.8 h. In the Krasnodar region of Russia, where many attempts are made to introduce guar, the length of daylight in May–June is 14.3–15.6 h. Meanwhile, the critical photoperiod for different guar varieties was reported as 12–13 h for earliest genotypes or 13–15 h for the late maturing ones. Under conditions of the prolonged photoperiod plants start flowering with a strong delay, although it has been found that some genotypes are almost insensitive to the photoperiod (Lubbers, 1987). Selection of the genotypes with weak PPS from the large intraspecific genetic diversity of guar may solve the problem of successful introduction of guar in temperate latitudes, as it was done for soybean (*Glycine max* (L.) Merrill). The selected soya genotypes with the weak PPS allowed to expand the area of the short-day legume crop cultivation from the tropics to the 50th parallel of the northern latitude (Watanabe et al., 2012).

To date, 115 viable seed accessions of different geographic origin are maintained at the VIR guar germplasm collection. The representativeness of the genetic diversity is comparable with the collections of the USA and India. The most accessions came from India, there are 4 accessions from Pakistan, 6 from Australia, 4 from the USA, 1 accession was obtained from the UK. The collection contains both breeding varieties and local landraces cultivated by farmers in India. The collection includes guar varieties of vegetable, fodder and grain use. 15 accessions of the guar collection represent the new breeding varieties and lines developed in recent years in Russia to solve the problem of import substitution of guar gum used in oil and gas industry.

Having available the collection of guar genetic resources, we investigated the variability of the photoperiodic reaction

of genotypes of different geographical origin, growing them on a provokingly long photoperiod. The aim was to get an idea about the range of variability of their speed of development and timing of the transition to flowering on the long day conditions.

Material and methods

We examined 192 guar genotypes that have been selected during our preliminary study of the guar genetic resources collection in 2017 at the Kuban branch of VIR (Krasnodar region, South of Russia, 45°02'55" N). The genotypes were selected on the basis of the most contrasting manifestation of morphological characters (days to flowering, days to first mature pod, plant height, number of basal shoots, resistance to diseases), as well as their geographical origin. In this representation mostly the local varieties from India as well as known cultivars from USA (Kinman, Lewis, Santa Cruz) were presented. In 2017 the selected 192 plants were marked with labels, and seeds from each of the plants were collected individually. Half of the seeds of the offspring of each plant was used for a field experiment of the following year (2018) at the Kuban branch of VIR, other half of the offspring of the same plants was used for the vegetation experiment in the conditions of the greenhouse of Pushkin branch of VIR (St. Petersburg region, 59°53'39" N).

As previously reported, the provocative long photoperiod causes the wider amplitude of variability in the photoperiod response among the guar genotypes studied (Lubbers, 1987). Thus, it becomes more likely to divide the studied population into groups that differ in their photoperiod sensitivity. In our experiments, the speed of transition to flowering of 192 guar lines was evaluated under greenhouse conditions at the Pushkin branch of VIR in natural daylight, corresponding to the St. Petersburg latitude. During the experiment the photoperiod decreased gradually from 18.2 to 18.9 h (May–June) with an average daytime temperature of +27 °C and a night temperature of +18.0 °C. Each of the 192 guar lines was sown in replications: two blocks with 4 plants in each (a total of 8 plants per line). For all the plants the date of appearance of seedlings (germination), the date of appearance of the first true leaf, the date of appearance of the first floral bud and the date of the first floral bud opening (the date of the flowering *per se*) were recorded individually.

With the replications available, for the date of appearance of the first true leaf the broad sense heritability coefficient (h^2) was calculated with Statistica 12 package using ANOVA as suggested by See et al. (2002):

$$h^2 = \frac{(\text{entry MS} - \text{error MS})/r}{\text{error MS} + (\text{entry MS} - \text{error MS})/r},$$

where r – number of replications, entry MS – Mean of Squares explained by a genotype.

At the Kuban branch of VIR the seeds of the same 192 lines were sown in rows of 2 m and 50 seeds per each line. At the end of the growing season (147 days after the sowing date) 10 plants were selected per each line, for them the total number of pods per plant and the percentage of

mature pods among them were calculated. The percentage of mature pods was considered as a “maturity index” estimated for each line.

Results

192 guar lines were sown under greenhouse conditions at the Pushkin branch of VIR in May 2018 at the daylight length of 18.2 h, and simultaneously sown in the field at the Kuban branch of VIR at the daylight length of 15.4 h. Only a few plants in the experiment at the Pushkin branch developed inferior pods that did not contain a single mature seed. A good-quality seed reproduction was obtained from all the plants grown under the conditions of the Kuban branch of VIR in Krasnodar region.

14 out of 192 lines at the Pushkin branch of VIR were excluded from the experiment because of a strong infection by *Fusarium* pathogen at the seedling stage. 12 of the remaining 178 lines of guar under the conditions of a long photoperiod did not go over to the generative stage, without even forming floral buds. The remaining 166 lines were represented in the experiment by 664 plants, the number of plants per line varied from 2 to 8 (due to the partial death of seedlings), an average of 4 plants per line.

In earlier studies, it was noted that the photoperiodic response of guar should not be assessed by the length of the period from germination to the appearance of the first flower. Photoperiodic sensitivity is only one of the factors that determine the speed of a plant's transition to flowering. For example, it was shown that the date of appearance of the first true leaf in guar significantly varies between genotypes. This trait affects the time of the appearance of the floral buds in different genotypes, and is not related to their PPS (Lubbers, 1987).

It was also established that genetic control of the transition to the generative phase in guar is carried out by two independent gene systems. The first gene system initiates the floral bud formation in response to a critical photoperiod, the second one determines the floral bud-opening when the corresponding critical photoperiod is achieved. These two phases of guar development determine how fast a plant goes through the stage of flowering, setting up the pods, maturing of seeds and the end of the vegetation (Lubbers, 1987).

Considering the previously published reports, we separately analyzed the variability of three components of the composite trait “days from germination to flowering”, which may potentially affect the early maturity of guar genotypes. In particular, the duration of three periods was investigated: (1) days from seedlings to first true leaf; (2) days from first true leaf to first floral bud; (3) days from first floral bud to first flower (floral bud-opening).

The variability of the trait

“days from seedlings to first true leaf”

For the most of lines studied, the number of days from seed germination to the first true leaf varied from 4 to 14 (Fig. 1). A few plants were found that developed the first leaf 28–32 days after seed germination, and then they successfully switched to the generative phase of formation floral buds and flowers. For lines that were represented in the experiment by

at least three plants, the effect of genotype on the variability of the analyzed trait was estimated by ANOVA, and turned out to be highly significant ($p < 10^{-6}$) (Table 1).

An attempt was also made to calculate the proportion of variability of this trait explained by genetic factors (heritability in a broad sense), using ANOVA (See et al., 2002). The calculated coefficient of heritability in the broad sense (h^2) was 0.46, thus, the variability of the length of period from seedlings appearance to first true leaf in guar is almost half determined by the genotype.

Variability of “days from first true leaf to first floral bud” and “days from first floral bud to first flower”

The experiment with guar growing in the greenhouse of the Pushkin branch of VIR was conducted from May to October with a photoperiod natural to the latitude of St. Petersburg. The experiment allowed us to observe the reaction of different genotypes of the short-day legume crop to a gradually decreasing length of daylight: from the maximum (~19 h) on the day of the summer solstice, to a relatively short (11 h) in the first decade of October. Since each guar genotype in the experiment required a certain critical photoperiod that triggers the transition to the generative phase, as the length of the light day shrank, the lines one by one passed to flowering as soon as the photoperiod reached a certain threshold level. This allowed us to divide all the plants into groups with the same PPS. Thus, according to the dates of transition to the stage of floral bud formation, the guar plants were divided into “early” and “late”, which formed the first floral bud with a day length of 17–18 and 12–13 h, respectively. At the same time, an intermediate group of plants was defined, in which the transition to floral bud formation was recorded at the 15-hour light day.

Since for all plants in the experiment, not only the date of the appearance of the first floral bud, but also the date of its opening (flowering) was recorded individually, some essential observations were made. Among the genetic diversity of the guar there were (i) genotypes that passed from floral bud formation to floral bud opening without delay (within 8 days); (ii) genotypes with delayed floral bud-opening. For those, from the moment a floral bud formation to first flower passed an average of 35 days, and in some cases, flowering did not occur even after 75 days.

Another important fact was recorded: on the long photoperiod, plants could have an equally short time interval between the first leaf and first floral bud (possible due to weak PPS), but at the same time, they differed greatly in the length of the

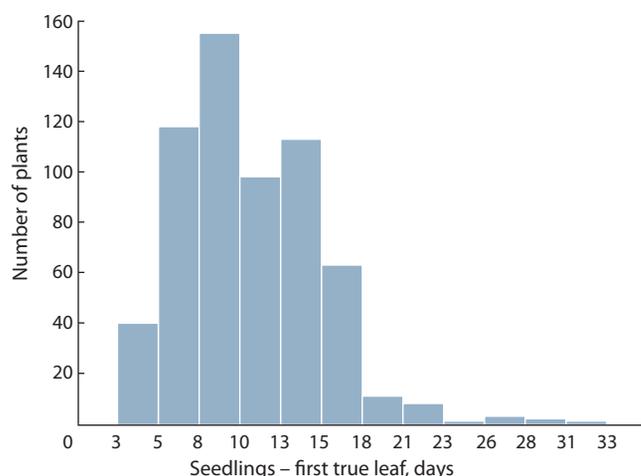


Fig. 1. The variability of the number of days from seedlings to first true leaf among the representation of guar genotypes of different geographical origin from the VIR collection.

period “seedlings – first true leaf” which significantly affected their flowering (first floral bud-opening) calendar date, as such. Thus, due to the delay of the vegetative development phase, plants can lately go over to floral bud formation, and, as a result, can be mistakenly classified as highly sensitive to photoperiod.

650 plants that have successfully switched to the generative phase under conditions of an extremely long photoperiod are arranged in Fig. 2 in order of increasing the time interval between the appearance of the first true leaf and the formation of the first floral bud. This time interval was considered in our experiment as the most accurate indicator of PPS. At the same time, for all plants in Fig. 2 days from seedlings to first true leaf and days from first floral bud to first flower are shown. Such a ranking made it possible to conditionally divide the entire sample into five groups.

The guar genotypes of the group 1 with the weakest PPS pass without delay to the formation of floral buds at a photoperiod of 18.6 h. They can be called “early” since: (i) only 34 days pass from the first leaf to first floral bud (Table 2); (ii) floral bud opening begins shortly after floral bud formation – on average, after 8 days. This means that an almost identical critical photoperiod is needed to trigger the floral bud formation and the floral bud opening.

The group 2 included “almost early” genotypes, which proceeded to the formation of floral buds when a daylight

Table 1. Results of analysis of variance (ANOVA) of the number of days from seedlings to first true leaf among the sample of guar genotypes

Effect	SS	df	MS	F	p-value
Intercept	64342.87	1	64342.87	4771.782	< 0.001
Genotype (a guar line)	6422.10	134	47.93	3.554	< 0.001
Error	6445.37	478	13.48		

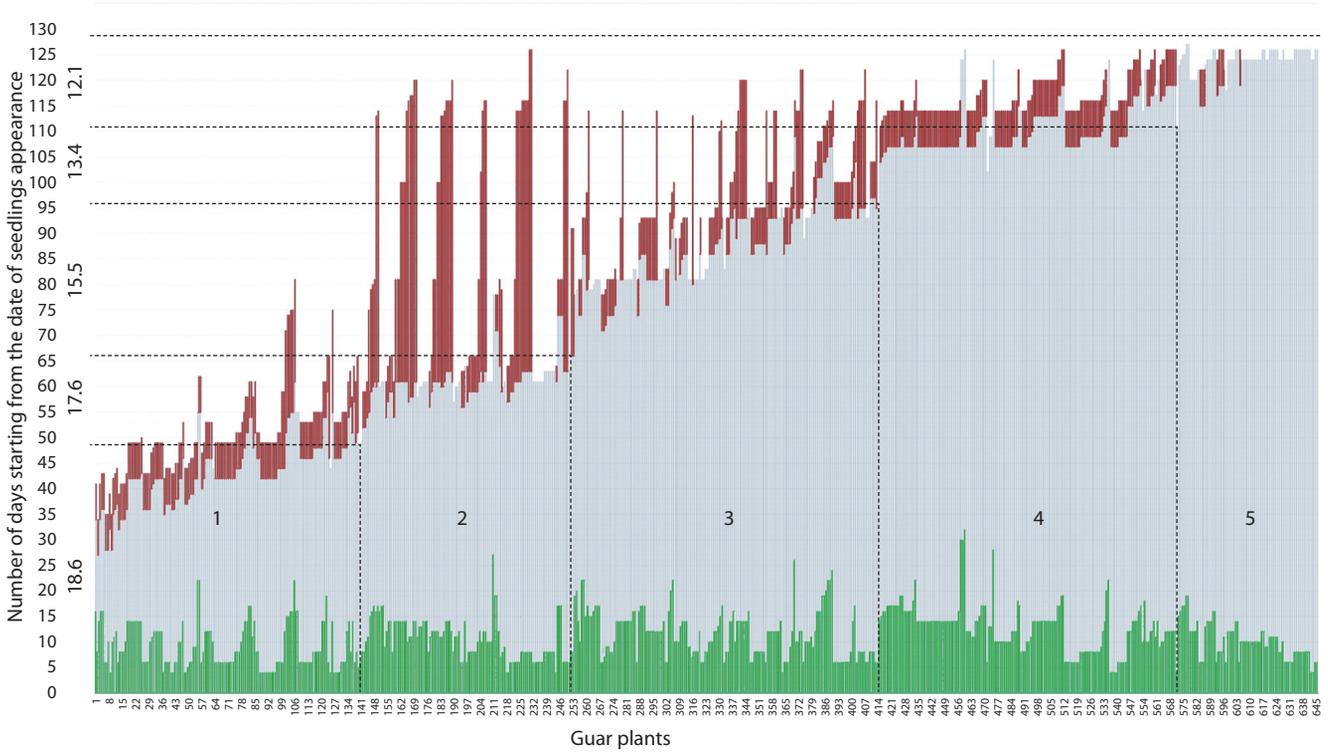


Fig. 2. The distribution of guar plants in groups No. 1–5, depending on the duration of the developmental stages and sensitivity to photoperiod. The dotted line shows the boundaries of the groups (average photoperiod values (h) are given for each group). The time interval from seedling appearance to first true leaf is marked in green for each plant, the period from the first true leaf to bud formation is marked in gray, floral bud formation to floral bud opening – in red.

Table 2. Description of the speed of development and the critical photoperiod required to trigger floral bud formation and floral bud opening for guar lines with different photoperiod sensitivity

Groups of guar based on PPS	Floral bud formation			Floral bud opening				
	Critical photoperiod, h	Period “first true leaf –floral bud formation”, days			Critical photoperiod, h	Period “first floral bud – floral bud opening”, days		
		mean	minimum	maximum		mean*	minimum	maximum
1	18.6	34±0.5	18	42	17.8	8±0.9	5	20
2	17.6	50±0.4	43	58	13.5	35±2.3	7	75/∞**
3	15.5	76±0.6	59	89	14.0	16±0.7	7	35/∞**
4	13.4	97±0.4	90	106	12.7	7±0.0	7	7
5	12.1	113±0.5	107	120	< 11	∞**	∞**	∞**

* The mean was calculated only for the plants, that passed to flowering.
** ∞ During the growing period no transition to flowering was recorded.

length did not exceed 17.6 h. A distinctive feature of this group is the delayed opening of the floral buds. Most of the plants formed their first floral buds in response to decreasing

of the photoperiod to 17.6 h, while the floral buds opened only in 35–40 days, when the length of the day decreased to 12.6 h. Some plants of this group did not switch to flowering

at all, having stopped at the stage of floral bud formation. Nevertheless, the average time interval between the first true leaf and the floral bud formation for these genotypes was only 50 days.

Genotypes of the very heterogeneous group 3 formed their first floral buds with a photoperiod of 15.5 h (approximately 76 days after the first leaf was appeared). The heterogeneity of the group is explained by the fact that some of the plants began to flower soon after budding (after 7–10 days), while for another part of the plants a photoperiod of 15.5 h was sufficient to form floral buds, but not for their opening. Thus, the launch of the actual flowering occurred when the day length was further reduced to 12 h. There were also some genotypes, which formed floral buds at 15.5 h, but did not open them at all.

The group 4 of “late” genotypes was quite homogeneous, the plants started budding when the day length reached 13.4 h, while the time interval between the first true leaf and the floral bud formation for these “late” genotypes was, on average, 97 days. The same length of the photoperiod seems to be critical for triggering the floral bud opening. As a result, almost all plants of this group opened their floral buds during the week after the bud formation.

The group 5 of “very late” genotypes formed their floral buds approximately 113 days after the first true leaf was developed, and the critical photoperiod for the floral bud formation was 12.1 h. Actually, no floral bud opening was recorded for most plants of this group.

Correlation of photoperiodic reaction of guar lines in greenhouse with their earliness in the field

Guar lines, which photoperiod sensitivity was tested in greenhouse conditions of the Pushkin branch of VIR with an extremely long day, were also studied in field conditions of Krasnodar region (at the Kuban branch of VIR). At the end of the field season, that is, 147 days after the planting date, for 10 plants of each line the percentage of mature pods (“maturity index”) was estimated. Since each line was assigned to one of five groups that differed in the PPS (Table 2), we had the opportunity to assess the significance of the difference in the “maturity index” of guar lines with different photoperiodic reactions.

Fig. 3 shows that the “late” and highly photoperiod sensitive lines from 4th and 5th groups showed also the latest maturation in the field conditions of the Krasnodar region. Nearly half of the pods of such plants did not mature at the time of harvesting. The probable reason for this can be the length of daylight (12–13 h) that is critical for this group of genotypes to start flowering (see Table 2). That threshold is not reached during the guar vegetation period under conditions of the Krasnodar area, where the daylight length in May–July is 14.3–15.4 h, 15.4–15.6 h and 14.7–15.6 h correspondingly (<https://voshod-solnca.ru>). Other lines of the groups 1–3, which require a photoperiod shorter than 15.5 h to go over to the generative stage, started flowering in Krasnodar area at the end of June, as soon as this length of daylight period is reached.

Discussion

To date, the only monograph by E.L. Lubbers (1987) is devoted to a detailed description of characterization and inheritance of photoperiodism in guar. It describes the results of experiments

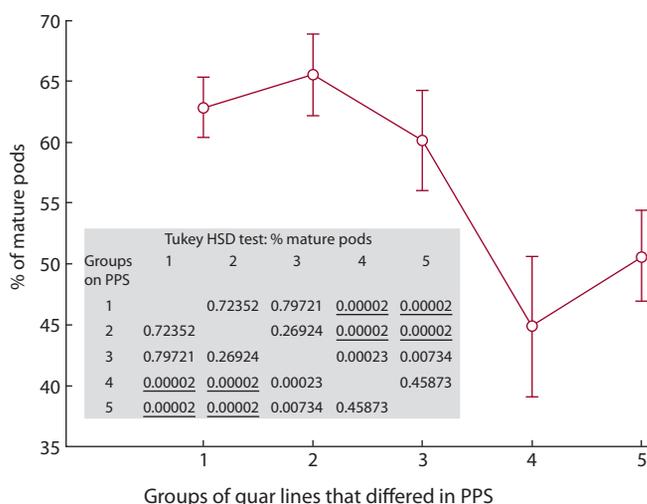


Fig. 3. Results of ANOVA showing significant difference in maturity index of the guar genotypes grown at the Kuban branch of VIR depending on their affiliation to the groups No. 1–5, registered at the Pushkin branch of VIR according to their photoperiod sensitivity.

with 330 guar genotypes, conducted in 1982–1983 in five geographical locations of the US (Arizona, Kansas and Texas), as well as the results of the evaluation of six guar varieties at different photoperiods under greenhouse conditions. It was found that, depending on the genotype, the critical length of daylight that triggers the transition to flowering in guar varies from 12 to 15 h. It should be noted that of the six varieties tested, one genotype was almost insensitive to the photoperiod, successfully proceeding to the flowering phase at 12, 13, 14 and 15 h of daylight.

In the author’s experiments with crossings of guar genotypes of the contrast PPS, the pattern of offspring segregation indicated the presence of two genes controlling “days from first true leaf to first floral bud” and two or three genes determining “days from first floral bud to first flower” in response to a certain photoperiod (Lubbers, 1987). Our results support the hypothesis about two independent gene systems that control the two stages of flowering in guar.

It can be assumed that in our experiment, the “early” and “late” lines of guar (groups 1–2 and 4–5 respectively, see Table 2) had alternative alleles of the genes of the first gene system responsible for the formation of floral buds in response to establishing of a critical photoperiod. Due to alternative alleles of the genes of the second gene system the groups 1 and 4 possibly switched to floral bud opening without regard to the length of the daylight, while groups 2 and 5 did it only in response to a certain critical photoperiod. Thus, it seems likely that in guar the reception of the length of the daylight, regulating the transition to flowering, occurs twice.

The combination of the alleles of these two gene systems may explain the diversity of dates of onset and passage of the generative phase observed among guar lines, when grown under conditions that are extremal for the short-day plant. For example, the plants of groups 1 and 4 were equally fast opening their floral buds, but the difference in the dates of

these floral buds' formation in these two groups was almost 60 days. At the same time, as followed from the analysis of variance presented in Fig. 3, the alleles of the genes that are responsible for initiation of floral bud formation have a major effect on early maturity.

Following Lubbers (1987), our observations of the variability of the period "seedlings – the first true leaf" indicate that photoperiodic sensitivity is only one of the factors that determine the speed of a plant's transition to flowering. When the photoperiodic sensitivity of guar is recorded as "days from seedlings to first flower", it might be masked by other unrelated factors, e. g. by different rates of passage of the vegetative development phases preceding flowering. In this regard, it is necessary to record not only the calendar actual date of the flowers appearance, but to take into account the date of the first true leaf appearance.

The observations of Lubbers (1987), as well as our results, confirm the idea that, although the photoperiodic reaction of guar limits the range of geographic latitudes in which this crop can be successfully grown, there is a real possibility to overcome this limitation by selecting and reproducing of nearly day-neutral genotypes from the existing genetic diversity of this species. The good perspective of such an approach of breeding a short-day legume crop adapted to conditions of temperate latitudes is well illustrated by the example of another short-day legume plant – soybean. Most soybean varieties need a short day to initiate flowering, but the successful breeding of genotypes with low sensitivity to the photoperiod has made possible the large-scale promotion of this crop to temperate latitudes (Watanabe et al., 2012).

There are many reasons for comparing the experience of the introduction of soya and guar. Although the genus *Cyamopsis* belongs to the tribe *Indigofereae* (Schrire, 2013), by the polymorphism of the chloroplast and mitochondrial genomes guar and soybeans belong to the same monophyletic clade on the phylogenetic tree of the subfamily *Faboideae*, along with *Phaseolus*, *Vigna*, *Dolichos* and other short-day legume crops (Cronk et al., 2006). A recent transcriptome study of the structure of the coding part of guar genome showed that *Glycine max* is the closely related species for guar, demonstrating the maximum percentage 41.91 % of homologous genes in these two species (Tanwar et al., 2017).

At least ten genes/QTLs have been reported controlling the transition to flowering and maturing for soybeans (Bernard, 1971; Cober et al., 2010; Kong et al., 2014; Kim et al., 2018). However, the progress in the identification and cloning of these genes is not obvious, which may be explained by the large number of genetic factors required for the initiation of the generative phase in legumes. The results of our research indicate that the phenotyping of guar plants in order to identify genetic loci that determine the speed of transition to flowering should include an analysis of all components of the period between date of the seedlings appearance and date of first flower, since each of them can be controlled by an independent gene system.

Conclusion

The transition to flowering in guar occurs in response to a critical photoperiod. Furthermore, the floral bud formation

may be triggered by the one certain length of daylight, but flowering per se (bud opening) – by another. In addition, the setting of floral buds also depends on genetic factors that determine the rate of seed germination and the formation of the first true leaf. In the VIR germplasm collection various guar genotypes are found that are insensitive to the photoperiod, both at the stage of formation of floral buds and at the bud opening. Genotypes with the lower photoperiod sensitivity are also early mature, showing the highest percentage of matured seeds by harvesting.

References

- Bernard R.L. Two major genes for time of flowering and maturity in soybeans. *Crop Sci.* 1971;11(2):242-244. DOI 10.2135/cropsci1971.0011183X001100020022x.
- Cober E.R., Molnar S.J., Charette M., Voldeng H.D. A new locus for early maturity in soybean. *Crop Sci.* 2010;50(2):524-527. DOI 10.2135/cropsci2009.04.0174.
- Cronk Q., Ojeda I., Pennington R.T. Legume comparative genomics: progress in phylogenetics and phylogenomics. *Curr. Opin. Plant Biol.* 2006;9(2):99-103. DOI 10.1016/j.pbi.2006.01.011.
- Gresta F., Cristaudo A., Trostle C., Anastasi U., Guarnaccia P., Catara S., Onofri A. Germination of guar (*Cyamopsis tetragonoloba* (L.) Taub.) genotypes with reduced temperature requirements. *Aust. J. Crop Sci.* 2018;12(6):954. DOI 10.21475/ajcs.18.12.06.PNE1049.
- Kim S.K., Kim E.S., Kim K.H., Jeong N., Lee J.S., Kang S. Genetic variance for flowering time conferring *E2* gene in photoperiod-insensitive early-maturing soybean accessions and topological distribution in Korea peninsula. *Mol. Breed.* 2018;38(12):148. DOI 10.1007/s11032-018-0887-x.
- Kong F., Nan H., Cao D., Li Y., Wu F., Wang J., Liu B. A new dominant gene *E9* conditions early flowering and maturity in soybean. *Crop Sci.* 2014;54(6):2529-2535. DOI 10.2135/cropsci2014.03.0228.
- Kuravadi N.A., Verma S., Pareek S., Gahlot P., Kumari S., Tanwar U.K., Tripathi S.K. Guar: an industrial crop from marginal farms. In: Bhullar G.S., Bhullar N.K. (Eds.) *Agricultural Sustainability: Progress and Prospects in Crop Research.* Acad. Press, 2012. DOI 10.1016/B978-0-12-404560-6.00003-4.
- Lubbers E.L. Characterization and Inheritance of Photoperiodism in Guar, *Cyamopsis tetragonoloba* (L.) Taub. Univ. of Arizona, 1987.
- Schrire B. A review of tribe Indigofereae (Leguminosae–Papilionoideae) in Southern Africa (including South Africa, Lesotho, Swaziland & Namibia; excluding Botswana). *S. Afr. J. Bot.* 2013;89:281-283. DOI 10.1016/j.sajb.2013.06.014.
- See D., Kanazin V., Kephart K., Blake T. Mapping genes controlling variation in barley grain protein concentration. *Crop Sci.* 2002;42(3): 680-685. DOI 10.2135/cropsci2002.6800.
- Startsev V.I., Livanskaya G.A., Kulikov M.A. Prospects of guar (*Cyamopsis tetragonoloba* L.) growing in Russia. *Vestnik Rossiiskogo Gosudarstvennogo Agrarnogo Zaochnogo Universiteta = Bulletin of the Russian State Agrarian Open University.* 2017;24:11-15. (in Russian)
- Tanwar U.K., Pruthi V., Randhawa G.S. RNA-Seq of guar (*Cyamopsis tetragonoloba*, L. Taub.) leaves: *de novo* transcrip-

tome assembly, functional annotation and development of genomic resources. *Front. Plant Sci.* 2017;8:91. DOI 10.3389/fpls.2017.00091.

Watanabe S., Harada K., Abe J. Genetic and molecular bases of photoperiod responses of flowering in soybean. *Breed. Sci.* 2012;61(5):531-543. DOI 10.1270/jsbbs.61.531.

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Acknowledgements. The study was financially supported by the Ministry of Education and Science of the Russian Federation, project RFMEFI60417X0168, Agreement No. 14.604.21.0168.

Conflict of interest. The authors declare no conflict of interest.

Received April 30, 2019. Revised May 21, 2019. Accepted May 22, 2019.