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The *WF1* (*White Flower 1*) gene controlling the white color of petals and flowering time in lines from a mapping population of flax (*Linum usitatissimum* L.)

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Flax (*Linum usitatissimum* L.) is grown in different climatic zones as both a spring and winter crop. Adaptation to different growing conditions produced genotypes with different growth durations and degrees of photosensitivity. It was always of great importance for breeders to create varieties with rapid development, in particular, early-flowering ones. The evaluation of lines from the VIR flax genetic collection revealed a wide intraspecific diversity in the duration of growth phases, the number of leaves on the stem (physiological indicator of early flowering), and the degree of photosensitivity. Line gc-109, early flowering under the long-day conditions, but greatly photosensitive, was found to possess the *wf1* (*white flowers*) gene, associated with early flowering and a small number of leaves. This line was crossed to the late-flowering but low-photosensitive line gc-375, which had reddish purple flowers. The analysis of segregation in F_2 held under the long (19 hours) and short (12 hours, daylength at the equator) day conditions showed that the number of leaves on the plant stem was associated with the flowering time and controlled by close genetic systems only under the long-day conditions. In addition, no relationship between the flowering time and petal color was found under the short-day conditions. Thus, different groups of genes are active in different light schedules. More than 200 lines of the 6th generation of inbreeding were obtained from the plants of the hybrid population. Their field testing under the long-day conditions showed that although the majority of the lines with white petals flowered early and had a small number of leaves, some of them bloomed later and were leafier. On the contrary, the early flowering and less leafy lines appeared among the lines with colored flowers. Therefore, it is reasonable to assume that a crossover between the gene participating in the control of early flowering, which came from the gc-109 line, and its *wf1* gene occurred in meiosis of F_1. The linkage between the genes controlling early flowering and white petals suggests that flower color can serve as a marker of early flowering in the selection of early breeding material.
Key words: flax; photosensitivity; earliness; flower color; linkage.

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Ген *WF1* (*White flower 1*) белоцветковости и сроки цветения линий картирующей популяции льна (*Linum usitatissimum* L.)

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Лен (*Linum usitatissimum* L.) выращивают в различных климатических зонах как яровую и озимую культуру. Приспособление к различным условиям произрастания привело к появлению генотипов с разным вегетационным периодом и различной степенью фоточувствительности. В то же время для селекционеров быстро развивающиеся, и в частности раноцветущие, сорта всегда имели большое значение. Изучение линий генетической коллекции льна ВИР выявило широкое внутривидовое разнообразие по продолжительности фаз вегетационного периода, числу листьев на стебле (физиологическому показателю раннего цветения) и степени фоточувствительности. У раноцветущей в условиях длинного дня, но сильно фоточувствительной линии гк-109 был идентифицирован ген белоцветковости *wf1*, ассоциированный с ранним цветением и малым количеством листьев. Эту линию скрестили с поздноцветущей, но слабо фоточувствительной линией гк-375, имеющей красно-фиолетовые цветки. При изучении расщепления F_2 в условиях длинного (19 ч) и короткого (12 ч – длина дня на экваторе) дня установлено, что число листьев на стебле растения ассоциировано со временем цветения и контролируется близкими генетическими системами только на длинном дне. Кроме того, на коротком дне не проявлялась связь между временем цветения и цветом лепестков. Таким образом, при разных режимах освещения активны разные группы генов. Из растений гибридной популяции было получено более 200 линий 6-го поколения инбридинга. Их тестирование в полевых условиях длинного дня показало, что хотя большинство белоцветковых линий зацветало рано и имело малое количество листьев, часть из них цвела поздно и была более облиственна. Среди линий с окрашенными цветками наоборот появились раноцветущие и малооблиственные. Таким обра-

зом, можно сделать вывод о том, что в мейозе F_1 произошел кроссинговер между геном, участвующим в контроле раннего цветения, пришедшим от линии гк-109, и ее геном *wf1*. Сцепление генов раннего цветения и белоцветковости свидетельствует о возможности использования цвета лепестков как маркера раннего цветения при отборе скороспелого селекционного материала.
Ключевые слова: лен; фоточувствительность; скороспелость; окраска цветка; сцепление.

Introduction

Cultivated plant *Linum usitatissimum* L. is spread all over the world in different climatic zones, latitudes, and elevations above the sea level. It is grown as a spring and winter crop. Anyway, the earliness of a variety is one of the most important agronomic characters. This species is characterized by wide ranges of total growth duration and the duration of its main phases: from germination till flowering and from flowering till ripening (Brutch et al., 2011). Being a quantitative character, the duration of flax vegetative period is under polygenic control (Brutch, 2011). The two growth phases are controlled by different genetic systems (Brutch, 2011). It means that each phase makes its own contribution and is important for crop earliness. Also, the number of leaves on the stem below the inflorescence is considered to be an indicator of flowering time in different plants (Obraztsov, 1983). This fact was also confirmed for flax, and a certain similarity between the inheritance patterns of flowering time and leaf number was discovered (Brutch, 2011).

Though the rate of plant development is influenced by many genes, it is interesting for breeders to search for morphological characters associated with earliness, because they can simplify the selection of breeding material. Such work was done at VIR on the basis of its flax genetic collection. It was discovered that in line gc-109, selected from the Argentine variety Macovi (k-6099), the gene *wf1* (*white flower 1*), controlling white filaments and petal color, was associated with early flowering (Porokhovinova, 2000). A specific feature of this gene is that it is semi dominant for corolla color. As a consequence, heterozygotes for this gene have diluted petal colors. This fact helps genotyping flowering plants. Due to this phenomenon, the association of the *wf1* gene with early flowering was confirmed, because plant development accelerated proportionally to the number of mutant alleles in the genome (Porokhovinova, 2000).

As mentioned above, flax is cultivated at different latitudes as both a spring and winter crop. It means that plants develop under different photoperiodic conditions. It was believed for long that *L. usitatissimum* was entirely a long-day species. However, evaluation of accessions from the VIR genetic collection revealed genotypes not influenced by the short 12-hour day (daytime at the equator). Also, the conducted experiments demonstrated a wide range of photosensitivity among the evaluated lines (Brutch et al., 2008). Previously it was found in many crops that the absence of photosensitivity could be used as an indicator of flowering earliness (Koshkin et al., 2003). But in contrast to other crops, it was discovered that flax had genotypes with all possible combinations of flowering earliness and photosensitivity degree, i. e. early flowering and low photosensitivity, late flowering and low photosensitivity, early flowering and high photosensitivity, late flowering and high photosensitivity (Brutch et al., 2008; Domantovich et al., 2012). It was detected in those experiments that line gc-109, being early in flowering under long-day conditions, was highly photosensitive. On the contrary, line gc-375, selected from the Egyptian accession Giza purple (k-6263), being rather late in flowering under long-day conditions, demonstrated relatively low photosensitivity (Domantovich at al., 2012). This line, in contrast to gc-109, had red-violet flowers. The discovery of this unique plant material allowed further genetic analysis of earliness, particularly, time of flowering.

The present paper is devoted to the evaluation of the flax flowering time inheritance, the number of leaves on the stem, and association of these characters with the white flower gene under long- and short-day conditions. Finally, the structure of the mapping population, consisting of self-pollinated lines selected from the hybrid between contrasting parents, is described.

Materials and methods

The experiments were carried out in Saint Petersburg, Russia, at 60° N. Two inbred lines from the VIR genetic collection, differing by several characters, were chosen for hybridization. Early-flowering and highly photosensitive line gc-109 was used as the female parent. It had white flowers controlled by the genotype *wf1wf1 SFC3-2SFC3-2 CSB1CSB1* (Porokhovinova, 2011). The male parent was late-flowering and low photosensitive line gc-375 with reddish purple flowers, controlled by the genotype *WF1WF1 sfc3-2sfc3-2 csb1csb1* (Porokhovinova, 2011). Both parents and F_1 and F_2 hybrids were tested for flowering time and degree of photosensitivity in a special facility with transparent glass and non-transparent pavilions. In the end of May, 10 seeds of each genotype were sown in 5-liter pots placed on mobile trolleys in two variants. During the germination–flowering time, the tested plants were exposed to the short-day (12 hours) conditions by moving the trolleys into the lightproof pavilion every day. For this time control plants were placed in the transparent pavilion. Thus, they remained under natural illumination (17.5–19 hours), and the influence of other environmental factors was equal for both plant groups. The date of the first flower opening was recorded for each plant, and the germination–flowering time was estimated. The average duration of this phase under long (T1) and short (T2) day conditions was calculated for each genotype. The coefficient of photoperiodic sensitivity (CPhPS) was calculated as CPhPS = T2/T1. When plants matured, leaves on stems below the inflorescence were counted.

Field experiments were conducted at the same geographic location. The F_3–F_6 families were grown in the field with individual isolation of the plants. Those showing segregation in petal color were rejected. For the next generation, seeds from only one plant from each family were chosen. Finally, about 200 lines that had no segregation within six years were selected and propagated. The created lines were evaluated in the field on 1 m long rows spaced by 0.1 m.

Evaluation of quantitative character inheritance is a very complicated task. Phenotypes are formed under the control of many genes whose expression is influenced by many en-

vironmental factors. In our experiment, the number of genes controlling the duration of the phase from germination to the opening of the first flower was analyzed by a computer program created by A.F. Merezhko (2005) on the Excel platform. The analyses were carried out individually for each year, characterized by specific weather conditions.

Statistical analysis of petal color association with quantitative characters was carried out using the bi-serial correlation coefficient:

$$r_{bs} = \frac{(x_{av1} - x_{av2})}{S_x} \sqrt{\frac{n_1 n_2}{N(N-1)}},$$

where x_{av1}, x_{av2} are the average character values for the groups with alternative colors; n_1, n_2 are the volumes of these groups; $N = (n_1 + n_2)$ is the sampling volume; S_x is the standard deviation for the whole sampling. The significance of r_{bs} was estimated by Student's *t*-test. The difference was considered significant when:

$$t_{\text{real}} = r_{bs} \sqrt{\frac{(N-2)}{(1-r_{bs}^2)}} \geq t_{\text{st}} \text{ for } k = N-2 \text{ and 5 \% significance level.}$$

Results

Several years of previous research showed that the early flowering parent gc-109 had high photosensitivity (CPhPS = = 1.26–1.45), and the late flowering, gc-375, low (CPhPS = = 0.95–1.07). High photosensitivity was dominant in F_1 (CPhPS = 1.28). The genetic analysis of flowering time performed with F_2 under the long-day conditions in 2008 revealed significant differences between the parental lines in two genes without dominance: one main gene and the other, 2.5 times weaker (Table 1). Exact determination of the number of genes controlling the number of leaves on the stem (physiological indicator of earliness) appeared to be impossible, but the most probable model of inheritance included three genes with the dominance degrees ranging from 0.0 to 0.5. One of the genes was 2.5 times stronger than the others. In addition, the correlation between the flowering time and the number of leaves on the stem in F_2 population under the long-day conditions was very close ($r = 0.91$). In 2009, the most reliable model of the flowering time genetic control included two genes with some epistasis, although a three-gene system was also probable (see Table 1). The inheritance of the leaf number character was very similar to that of the first variant of flowering time inheritance (see Table 1). The correlation between the flowering time and the number of leaves on the stem was 0.50. Thus, it can be supposed that the flowering time and the number of leaves are substantially determined by the same genes.

In 2008, the parental lines grown under the short-day conditions differed significantly from each other in five genes determining flowering time (Table 2). The first one was three times stronger than the others and had a partial dominance (–0.5) of early flowering. The inheritance of the leaf number on the stem was close to a three-gene model. One of these genes was four times stronger than the others. The correlation between flowering time and the number of leaves on the stem in the F_2 population was 0.57. In 2009, flowering time inheritance was close to a four-gene model in which one gene influenced the character three times stronger than the others, and the second, two times stronger than the remaining two genes. Leaf number inheritance also corresponded to a four-gene model where only one gene was 1.5 times as strong as the others. The correlation between flowering time and the number of leaves on the stem was 0.38. Thus, it is reasonable to

Table 1. Character inheritance under the long-day conditions in F_2 of the gc-109 × gc-375 hybrid in 2008 and 2009

Year	Number of genes	Dominance	Influence of genes	Epistasis	χ^2 observed	χ^2 theoretical
Developmental phase: from germination to the first flower opening						
2008	2	A = B = 0	A = 2.5; B = 1.0	No	5.48*	5.99
2009	2	A = 1.0; B = 0.4	Equal	B > A = 0.3	0.83*	3.84
	3	A = B = 1.0; C = 0.4		No	1.91*	3.84
Number of leaves on the stem						
2008	3	A = 0.5; B = 0.3; C = 0.0	A = 2.5; B = C = 1.0	No	1.00	0.00
2009	2	A = B = 1.0	A = 1.8; B = 1.0	No	4.43	3.84

A, B, C – gene symbols.
* Inheritance model is statistically significant.

Table 2. Character inheritance under the short-day conditions in the gc-109 × gc-375 hybrid in 2008 and 2009

Year	Number of genes	Dominance	Influence of genes	Epistasis	χ^2 observed	χ^2 theoretical
Developmental phase: from germination to the first flower opening						
2008	5	A = 0.5; B = C = D = E = 0.0	A = 3.0; B = C = D = E = 1.0	No	0.00*	0.00
2009	4	A = B = C = D = 1.0	A = 3.0; B = 2.0; C = D = 1.0	No	12.7	5.99
Number of leaves on the stem						
2008	3	A = 0.2; B = C = 0.0	A = 4.0; B = C = 1.0	No	4.37	0.00
2009	4	A = B = C = 1.0; D = 0.0	A = 1.5; B = C = D = 1.0	No	5.45*	5.99

A, B, C – gene symbols.
* Inheritance model is statistically significant.

Table 3. Comparison of genotypic classes in the segregation for quantitative characters in F_2 of the gc109 × gc375 hybrid under the long-day conditions in 2008

Characters of the 1st genotype			Characters of the 2nd genotype			t_{real}	t_{st}	r_{bs}	t_{real}	t_{st}
Genotype	$x_{av} \pm mx$	*n*	Genotype	$x_{av} \pm mx$	*n*					
Phase from germination to the first flower opening										
WF1WF1	47.1 ± 0.50	30	*WF1wf1*	44.7 ± 0.40	57	3.72*	2.00	0.37	3.62*	1.96
WF1wf1	44.7 ± 0.40	57	*wf1wf1*	43.1 ± 0.57	26	2.30*	2.00	0.24	2.26*	1.96
WF1WF1	47.1 ± 0.50	30	*wf1wf1*	43.1 ± 0.57	26	5.26*	2.00	0.58	5.28*	1.96
Number of leaves on the stem										
WF1WF1	102.7 ± 2.32	30	*WF1wf1*	88.2 ± 2.16	57	4.59*	2.00	0.23	2.14*	1.96
WF1wf1	88.2 ± 2.16	57	*wf1wf1*	79.9 ± 3.18	26	2.15*	2.00	0.62	5.89*	1.96
WF1WF1	102.7 ± 2.32	30	*wf1wf1*	79.9 ± 3.18	26	5.79*	2.00	0.42	4.25*	1.96

* Difference between groups is statistically significant.

Table 4. Comparison of genotypic classes in the segregation for quantitative characters in F_2 of the gc109 × gc375 hybrid under the short-day conditions in 2008

Characters of the 1st genotype			Characters of the 2nd genotype			t_{real}	t_{st}
Genotype	$x_{av} \pm mx$	*n*	Genotype	$x_{av} \pm mx$	*n*		
Phase from germination to the first flower opening							
WF1WF1	59.4 ± 0.86	52	*WF1wf1*	58.3 ± 0.55	89	1.06	2.00
WF1wf1	58.3 ± 0.55	89	*wf1wf1*	57.4 ± 0.75	48	0.95	2.00
WF1WF1	59.4 ± 0.86	52	*wf1wf1*	57.4 ± 0.75	48	1.72	2.00
Number of leaves on the stem							
WF1WF1	146.7 ± 2.45	52	*WF1wf1*	145.4 ± 2.43	89	0.38	2.00
WF1wf1	145.4 ± 2.43	89	*wf1wf1*	139.7 ± 3.97	48	1.22	2.00
WF1WF1	146.7 ± 2.45	52	*wf1wf1*	139.7 ± 3.97	48	1.50	2.00

conclude that the differences between the inheritance models of flowering time and the leaf number were more substantial under the short-day conditions than under long-day ones.

Further analysis of the previously identified association between the *wf1* gene controlling white petals (from line gc-109, Argentina) with early flowering in the F_1 generation showed that the expression of this gene correlated with early flowering and small number of leaves only under the long-day conditions. Thus, the results indicate that at different light-dark schedules, different genes controlling flowering time and the number of leaves on the stem are expressed. The gene(s) controlling early flowering and associated with the *wf1* gene does (do) not function under the short-day conditions.

Analyses of the F_2 segregation of *wf1* gene alleles according to petal color showed that the recessive allele was associated with early flowering and fewer leaves only under the long-day conditions (Tables 3–6). In 2008, the differences in flowering time between genotypes *WF1WF1*, *WF1wf1 and wf1wf1* under the long-day conditions were statistically significant, although *WF1wf1* plants bloomed only one day later than *wf1wf1* ones (see Table 3). In 2009, the first flower opening was synchronous with the last two genotypes (see Table 5). The same results were obtained for the number of leaves on the stems under the long-day conditions in 2008 and 2009 (see Tables 3, 5). Under the short-day conditions, significant differences between genotypes were found in neither flowering time nor the number of leaves (see Tables 4, 6). These results confirm that the gene involved in the control of flowering time and associated with the *wf1* gene functions only under long-day conditions.

Evaluation of F_3 families under the long-day field conditions showed that the segregation in the hybrid population resulted in the appearance of families with white flowers characterized by both early and relatively late flowering time. Also, early-flowering families appeared among families with colored flowers. Families heterozygous for this gene were divided into two groups: in the first the segregation in further generations showed significant association of the flowering time with petal color; whereas no such relationship was observed in the other. This suggests that one of the genes involved in the control of early flowering under the long-day conditions was linked to the *wf1* gene. As a result of chromosomal crossover, recombination occurred in several descendant families.

A set of about 200 I_6 lines was evaluated in the field under the natural long-day conditions in 2018. The groups of lines with white and colored flowers were not equal in size, so the results are presented as percentages of genotypes with approximately equivalent quantitative characters. The majority of the lines with white flowers were early flowering ones, and those that had colored flowers generally flowered later (Figure, *a*).

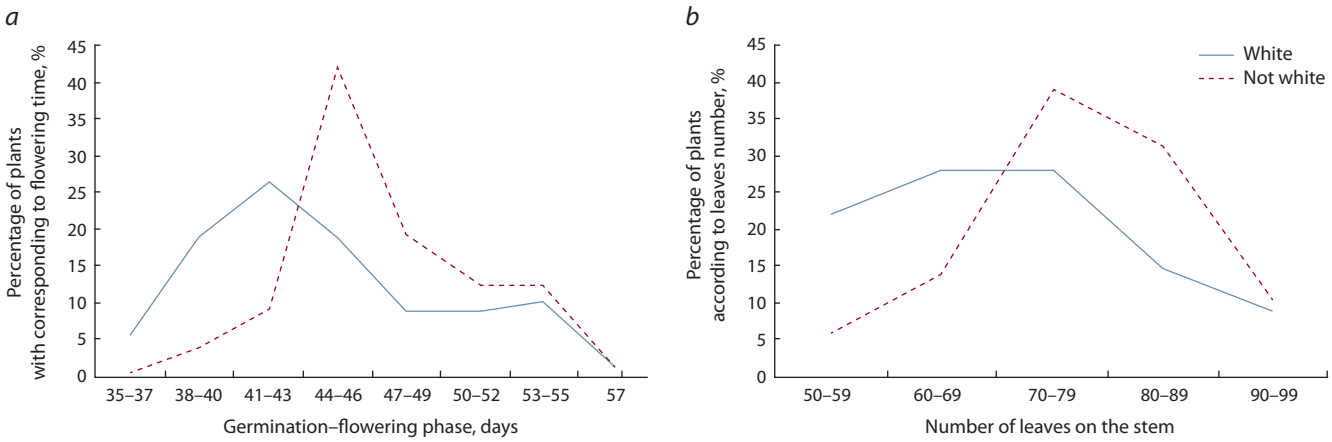
Table 5. Comparison of genotypic classes in the segregation for quantitative characters in F_2 of the gc109×gc375 hybrid under the long-day conditions in 2009

Characters of the 1st genotype			Characters of the 2nd genotype			t_{real}	t_{st}	r_{bs}	t_{real}	t_{st}
Genotype	$x_{av} \pm mx$	*n*	Genotype	$x_{av} \pm mx$	*n*					
Phase from germination to the first flower opening										
WF1WF1	55.9±0.42	64	*WF1wf1*	51.9±0.42	106	6.26*	2.00	0.44	6.26*	1.96
WF1wf1	51.9±0.42	106	*wf1wf1*	52.2±0.47	64	0.43	2.00	–	–	1.96
WF1WF1	55.9±0.42	64	*wf1wf1*	52.2±0.47	64	5.86*	2.00	0.44	6.06*	1.96
Number of leaves on the stem										
WF1WF1	88.7±2.45	58	*WF1wf1*	80.2±1.73	103	2.85*	2.00	0.22	2.85*	1.96
WF1wf1	80.2±1.73	103	*wf1wf1*	81.2±1.79	60	0.37	2.00	–	–	1.96
WF1WF1	88.7±2.45	58	*wf1wf1*	81.2±1.79	60	2.47*	2.00	0.93	26.52*	1.96

* Difference between groups is statistically significant.

Table 6. Comparison of genotypic classes in the segregation for quantitative characters in F_2 of the gc109×gc375 hybrid under the short-day conditions in 2009

Characters of the 1st genotype			Characters of the 2nd genotype			t_{real}	t_{st}
Genotype	$x_{av} \pm mx$	*n*	Genotype	$x_{av} \pm mx$	*n*		
Phase from germination to the first flower opening							
WF1WF1	66.1±0.94	52	*WF1wf1*	65.7±0.70	117	0.33	2.00
WF1wf1	65.7±0.70	117	*wf1wf1*	63.8±0.86	64	1.69	2.00
WF1WF1	66.1±0.94	52	*wf1wf1*	63.8±0.86	64	1.83	2.00
Number of leaves on the stem							
WF1WF1	113.5±3.01	49	*WF1wf1*	115.2±1.78	103	1.32	2.00
WF1wf1	115.2±1.78	103	*wf1wf1*	110.7±2.96	64	1.40	2.00
WF1WF1	113.5±3.01	49	*wf1wf1*	110.7±2.96	64	0.65	2.00



Distribution of lines with white and colored flowers according to their germination–flowering phase duration (*a*) and the number of leaves on the stem (*b*) in field conditions. Leningrad Province, 2018.

This was also true of the number of leaves (see Figure, *b*). In general, the correlation between the time of flowering and the number of leaves was retained ($r = 0.74$) within this sampling, because the experiment was conducted under the long-day conditions. The association of petal color with the time of flowering and the number of leaves on the stem was also still significant (Table 7). However, as already found for F_3 generation, some genotypes expressed other phenotypes. Some white-flowered lines were very late in blooming, and several lines with colored petals were very early.

Table 7. Comparison of genotypic classes in the segregation for quantitative characters in lines selected from the gc109 × gc375 hybrid under long-day field conditions in 2018

Characters of the 1st genotype			Characters of the 2nd genotype			t_{real}	t_{st}	r_{bs}	t_{real}	t_{st}
Genotype	$x_{av} \pm mx$	*n*	Genotype	$x_{av} \pm mx$	*n*					
Phase from germination to the first flower opening										
WF1-	47.3 ± 0.56	134	*wf1wf1*	44.5 ± 0.65	68	3.76*	2.00	0.28	4.14*	1.96
Number of leaves on the stem										
WF1-	76.6 ± 3.05	134	*wf1wf1*	70.2 ± 2.13	68	3.84*	2.00	0.27	4.03*	1.96

* Difference between groups is statistically significant.

Conclusion

Evaluation of the lines selected from the hybrid between the early flowering line gc-109 with white petals and the late-flowering gc-375 with reddish purple petals showed that one of the genes involved in the control of flowering time under the long-day conditions was linked to the white flower gene *wf1*. This marker can be used for the detection of early flowering genotypes in hybrid populations. It can be especially useful in cases when the progeny is grown under abnormal conditions (green house, etc.) when the real flowering earliness is not evident. In addition, the white color of petals indicates the high probability of earliness gene homozygosity.

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