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Research Article



Genetic diversity of barley accessions from Mongolia for greenbug resistance

Evgeny E. Radchenko¹, Renat A. Abdullaev¹, Daria E. Akimova¹, Irina Yu. Zajtseva²

¹ N.I. Vavilov All-Russian Institute of Plant Genetic Resources, Saint Petersburg, Russia;

² Saint Petersburg State Agrarian University, Saint Petersburg, Russia

BACKGROUND: Significant damage to barley crops in the southern regions of the Russian Federation is caused by the greenbug *Schizaphis graminum* Rondani. Cultivation of resistant varieties is a cheap, efficient and environmentally friendly way to combat the phytophage. The specificity of relations between *S. graminum* and barley is shown, that determines the need to broaden the genetic diversity of cultivated varieties.

AIM: The study of effectiveness and genetic control of the greenbug resistance in barley accessions from Mongolia.

MATERIALS AND METHODS: We studied 175 barley landraces from Mongolia for resistance to the Krasnodar aphid population. We assessed damage to resistant lines selected from heterogeneous accessions k-3885, k-3904, and k-4080, as well as the variety Post (a carrier of the previously identified *Rsg1* gene) by 86 aphid clones isolated from the population. Under laboratory conditions, the aphid resistance segregation of F₂ hybrids was analyzed from crossing three accessions from Mongolia with a susceptible tester.

RESULTS: Five heterogeneous accessions were identified, in which plants with high resistance to the pest were found; in 28 accessions, damage to the leaf surface of the resistant component varied from 31% to 60%. As a result of the assessment of the resistance of four barley accessions to *S. graminum* clones, 15 virulence phenotypes were identified. Accessions k-3885, k-3904 and k-4080 each have one dominant resistance allele, which differ from each other and differ from *Rsg1*.

CONCLUSIONS: The genetic diversity of barley accessions from Mongolia in terms of greenbug resistance is low. The genotypes of *S. graminum* differentially interact not only with the major, but also with weakly manifested barley resistance genes.

Keywords: barley; *Schizaphis graminum* Rondani; resistance; genes.

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Научная статья

Генетическое разнообразие образцов ячменя из Монголии по устойчивости к обыкновенной злаковой тле

Е.Е. Радченко¹, Р.А. Абдуллаев¹, Д.Е. Акимова¹, И.Ю. Зайцева²¹ Федеральный исследовательский центр Всероссийский институт генетических ресурсов растений им. Н.И. Вавилова, Санкт-Петербург, Россия;² Санкт-Петербургский государственный аграрный университет, Санкт-Петербург, Россия

Актуальность. Значительный ущерб посевам ячменя в южных регионах Российской Федерации причиняет обыкновенная злаковая тля *Schizaphis graminum* Rondani. Возделывание устойчивых сортов — дешевый, эффективный и экологически безопасный способ борьбы с фитофагом. Специфичность отношений *S. graminum* с ячменем определяет необходимость расширения генетического разнообразия возделываемых сортов.

Цель — исследование эффективности и генетического контроля устойчивости образцов ячменя из Монголии к обыкновенной злаковой тле.

Материалы и методы. Изучили 175 образцов местного ячменя из Монголии по устойчивости к краснодарской популяции тли. Оценили поврежденность устойчивых линий, отобранных из гетерогенных образцов к-3885, к-3904 и к-4080, а также сорта Post (носителя идентифицированного ранее гена *Rsg1*), выделенными из популяции 86 клонами тли. В лабораторных условиях анализировали расщепление по устойчивости к тле гибридов F₂ от скрещивания трех образцов из Монголии с восприимчивым тестером.

Результаты. Выделили 6 гетерогенных образцов, у которых выявлены растения с высокой устойчивостью к вредителю; у 28 образцов поврежденность листовой поверхности устойчивого компонента варьировала от 31 до 60 %. В результате оценки устойчивости четырех образцов ячменя к клонам *S. graminum* выявили 15 фенотипов вирулентности. Образцы к-3885, к-3904 и к-4080 имеют по одному доминантному аллелю устойчивости, которые различаются между собой и отличаются от *Rsg1*.

Выводы. Генетическое разнообразие образцов ячменя из Монголии по устойчивости к обыкновенной злаковой тле невысоко. Генотипы *S. graminum* дифференциально взаимодействуют не только с главными, но и со слабо проявляющимися генами устойчивости ячменя.

Ключевые слова: ячмень; *Schizaphis graminum* Rondani; устойчивость; гены.

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BACKGROUND

The greenbug *Schizaphis graminum* Rondani has caused significant damage to barley crops in the southern regions of the Russian Federation. The degree of harmfulness of the insect depends on the timing of plant colonization (the insects cause the most significant damage to winter and spring crops when migrating to the fields in the germination phase) and the abundance and duration of feeding of the phytophage [1]. The aphid's harmfulness to barley can be significantly limited using the breeding and cultivation of resistant varieties. The specificity of the relationships between *S. graminum* and host plants, including barley, has been investigated previously [2]. However, the ability of *S. graminum* to adapt to a resistant host determines the need for a constant search for new resistance donors for breeding.

To date, only four alleles of two genes have been identified that control barley's resistance to individual biotypes of the greenbug in the USA. Back in 1945, I.M. Atkins and R.G. Dahms [3] identified two Korean varieties of winter barley, Omugi and Dobaku, which showed high heritability of the resistance trait. Various commercial barley varieties have subsequently been produced using Omugi. An analysis of the inheritance of aphid resistance showed that the Omugi, Dobaku, Derbent, Kearney, and Will varieties have a common dominant resistance allele, subsequently designated *Rsg1a*, and then *Rsg1* [4–7]. According to the results of trisomic analysis, the Will resistance gene is localized in the centromeric segment of chromosome 1 [7]. With the use of molecular markers, the *Rsg1* locus was mapped on the long arm of chromosome 3H [8]. The Post variety was selected from the Harrison × Will hybrid population by individual selection [9]; however, the heterogeneity of this variety in terms of resistance to the aphid necessitated the selection of the Post 90 variety [10]. The *Rsg1a* gene is effective against aphid biotypes B–G, I–K, CWR, and WWG, but not against biotype H [11–14].

The dominant allele *Rsg2b*, which confers resistance to the same aphid biotypes as *Rsg1a*, was identified in a native barley accession from Pakistan, PI 426756 [11, 14, 15]. The expression of the *Rsg2b* gene is somewhat lower than that of *Rsg1a*; therefore, the Post 90 variety is preferable for breeding [16]. In subsequent experiments, PI 426756 was found to be more resistant than Post 90 to biotype E [17]. In addition, the *Rsg2b* gene, in contrast to *Rsg1a*, is effective against the aphid TX1 isolate, where a differential interaction between the insect and the host plant was noted. Based on this, new gene symbols, *Rsg1* and *Rsg2*, have been proposed. The variety Wintermalt, which is susceptible to all other intraspecific forms of the insect, is weakly damaged by the G and J biotypes [12, 14]. Resistance to biotype G is also possessed by the Coulter and Bancroft varieties,

which are recommended for breeding [18]. However, the Wintermalt and Coulter varieties are severely damaged by the TX1 aphid biotype [17].

The complexity of the *Rsg1* locus has now been identified, where an accession of *Hordeum vulgare* ssp. *spontaneum* WBDC336 (PI 682028) had the *Rsg1.a3* allele, which provides resistance to biotypes C, E, H, I, WY81, WY12 MC, and WY86 of the greenbug [19]. It was also established that the accession of *H. vulgare* ssp. *spontaneum* WBDC053 (PI 681777) carried the *Rsg2.a3* allele either closely linked or allelic to *Rsg2*. WBDC053 is resistant to biotypes B, C, E, I, TX1, WY4A, WY4B, WY81, WY12MC, and WY86, but is severely damaged by aphid biotypes F, H, WY10MC, and WY10B [20].

Accessions of local barley represent a rich source of replenishment of the bank of effective resistance genes to *S. graminum*. Thus, among the accessions from East and South Asian countries, heterogeneous forms were identified that differed in the level of resistance to the Krasnodar population of the insect. The high resistance of 98 accessions is controlled by alleles that are not identical to *Rsg1*. As a result of the testing of 150 accessions from Mongolia, three heterogeneous forms were identified, among which, two accessions contained plants with high resistance and one accession contained plants with moderate resistance to the aphid [21].

The experiments mentioned above were performed in 2002–2004 using the Krasnodar aphid population. The level of resistance of Mongolian barley accessions to new populations of *S. graminum* almost 20 years later is an interesting question. In this work, we study the efficiency and genetic control of aphid resistance in barley accessions isolated in previous experiments.

MATERIALS AND RESEARCH METHODS

We studied the resistance to the Krasnodar (branch of the N.I. Vavilov All-Russian Institute of Plant Genetic Resources, Kuban experimental station (KES VIR, Gulkevichsky district) population of the greenbug in 175 barley accessions from Mongolia. In addition, the resistance of the Post cultivar (k-31204, USA), containing the previously identified *Rsg1* resistance gene, and lines selected from heterogeneous Mongolian accessions (k-3885, k-3904, and k-4080) were evaluated. Segregation in resistance to *S. graminum* of F_2 hybrids resulting from crossing the selected forms with the susceptible variety Belogorskiy (k-22089, Russia, Leningrad region) was also analyzed.

The work was performed in a light room, where the air temperature was maintained at 20°C–25°C. Insects for laboratory experiments were collected on sorghum crops from KES VIR in July (the period of maximum pest abundance). A susceptible accession of sorghum was used [*Sorghum bicolor* (L.) Moench] SLV-2, as well as

the varieties Efremovskoe beloe and Kubanskoe krasnoe 1677, which are moderately resistant to aphids.

In the laboratory, the collected samples of the aphid were cloned. Sprouted barley seeds of the Belogorskiy variety were laid out on cotton wool moistened with water, placed in halves of Petri dishes, then one female was placed on each seedling, and the dish was covered with a glass cage, while the upper part was covered with silk bolting cloth. Cages with aphid clones were placed on light units equipped with fluorescent lamps. Thirty-five clones were collected from the SLV-2 accession, 29 clones were collected from Kubanskoe krasnoe 1677, and 22 clones were collected from Efremovskoe beloe.

To assess the resistance of the barley accessions, the seeds were sown in rows in plastic flats filled with a non-sterile soil mixture. Two rows of susceptible control (variety Belogorskiy), 10 rows of tested forms, and 1 row of cultivar Post were sown. Juvenile plants were infested with a mixture of clones, and aphids of different ages were shaken off (4–5 ind./plant) on the barley accessions tested. At the feeding site of *S. graminum*, plant tissues become necrotic, which enables us to test the plant damage. When the control died (usually on day 10–14 after infestation), the resistance was assessed on a scale from 0 (no damage) to 10. Plants with scores of 1–4 (damaged up to 30% of the leaf surface) were classified as resistant, while those with scores of 9–10 were classified as susceptible [22]. The samples identified as resistant were then tested again.

Damage to the Post variety and three resistant barley lines from Mongolia were assessed using 86 aphid clones. For this purpose, experimental accessions and the susceptible control were sown in vessels with soil in a circular order and covered with glass cages. Seedlings were infested with aphids of the same clone at a rate of five individuals per plant, and when the control died, the resistance of plants was assessed according to the scale described above. If the results were not clear, the experiment was repeated.

To determine the number and nature of the interactions of the resistance-controlling genes, the resistant lines k-3885, k-3904, and k-4080 (maternal forms) and the non-resistant variety Belogorskiy (paternal form) were crossed. Segregation of F₂ hybrids for aphid resistance was analyzed in a laboratory. Seeds were sown in rows in plastic flats containing soil. One row each of P₁, P₂, and F₁, and 7–8 rows of F₂ were sown. The F₂ seeds were the offspring of a single F₁ plant. Weak or late-sprouting plants were removed 2–3 days after germination. When the second leaf appeared, the hybrids were infested by the aphid (a clone avirulent to resistant lines) at a rate of four individuals per plant. The flats were examined after 2 days and, if necessary, additional infestation was performed. During the period of death of a susceptible parent, the damage to hybrids was assessed. To reduce classification errors of phenotypes, two counts were usually performed: one when approximately 70% of the plants of a susceptible form had died off and one after 2–3 days, when only single plants of the Belogorskiy variety were characterized by a damage score of 9. Plants similar to the paternal form (scores of 9 or 10) were considered homozygous non-resistant (S). The resistant class (R) included plants with similar degrees of damage as the maternal form. To determine the correspondence between the obtained (observed) and theoretically expected data, the χ^2 test was used.

RESULTS AND DISCUSSION

The results of the assessment of resistance of the collection of barley accessions from Mongolia to the “old” and “new” populations of *S. graminum* generally coincided (Table 1). In 2021, a larger number of accessions was noted, where plants with high (3 points) resistance to the pest were identified. Apparently, these accessions were not isolated in 2004 due to the low frequency of this phenotypic class. In 2021, 28 heterogeneous accessions were identified, in which the manifestation of the

Table 1. Barley accessions from Mongolia, distinguished by their resistance to the greenbug, *S. graminum*

VIR catalogue number	Accession	Variety	Resistance, score	
			2004	2021
3885	Landrace	<i>Pallidum, coeleste, violaceum, himalayense</i>	4–6, 8, 9	7–9
3904	«	<i>Coeleste</i>	4–6, 8, 9	5, 7, 8
3926	«	<i>Pallidum</i>	10	3, 7, 8
4080	«	<i>Coeleste, revelatum</i>	5, 7–10	4–10
21731	«	<i>Revelatum, coeleste</i>	10	3, 8, 10
21737	«	<i>Coeleste</i>	6, 7	3, 7, 8
22089		Belogorskiy (control)	9, 10	9, 10

Table 2. Frequency of virulent to barley accessions *S. graminum* clones collected on three sorghum varieties (%)

Barley accession	Sorghum variety		
	SLV-2	Efremovskoe below	Kubanskoe krasnoe 1677
Post	22.9	40.9	41.4
k-3904	20.0	31.8	44.8
k-4080	25.7	54.5	55.2
k-3885	28.6	45.5	48.3

Table 3. Phenotypic diversity of the Krasnodar population of *S. graminum*

Virulence phenotype	Phenotype frequency, %	Barley accessions			
		Post	k-3904	k-4080	k-3885
1	34.8	R	R	R	R
2	7.0	S	R	R	R
3	2.3	R	S	R	R
4	4.6	R	R	S	R
5	7.0	R	R	R	S
6	7.0	R	R	S	S
7	1.2	S	S	R	R
8	3.5	R	S	S	R
9	3.5	S	R	R	S
10	1.2	S	R	S	R
11	7.0	R	S	S	S
12	3.5	S	R	S	S
13	1.2	S	S	R	S
14	4.6	S	S	S	R
15	11.6	S	S	S	S

Note. R — resistance, S — accession susceptibility.

resistant component varied within 5–7 points (31%–60% of the leaf surface was damaged).

The significant variability of the trait may be due to the manifestation of genes with low expressivity and/or the presence of clones with different virulence to the studied forms in the *S. graminum* population. The infestation of pure lines isolated from heterogeneous accessions (k-3885, k-3904, and k-4080) with a mixture of clones (population) of aphids caused plant damage with scores of 2–8 points. When these lines were infested with insect clones, three phenotypic classes were noted: resistant (1–4 points, manifestation of genes with high expressivity in this accession to this clone), moderately resistant (5–8 points, the action of genes with a weak phenotypic manifestation), and susceptible (9–10 points, virulence of this clone to both major and minor resistance genes). Consequently, both hypotheses were confirmed, where lines protected by aphid resistance genes with a distinct and poor phenotypic manifestation, which differentially interact with insect genotypes, were identified.

The frequency of the detection of aphid clones virulent to barley accessions with clearly manifested resistance genes on sorghum varieties differed significantly, as when feeding in the field on moderately resistant sorghum varieties, there was a clear accumulation in comparison with the susceptible accession SLV-2 (an excess of 1.6–2.2 times) of *S. graminum* clones that were virulent to the barley accessions (Table 2). The efficiency of the resistance genes was low, as 32%–45% of the clones in the Krasnodar insect population are virulent to accessions from Mongolia and to the Post cultivar.

As a result of the assessment of resistance of four accessions of barley to 86 clones of *S. graminum*, 15 virulence phenotypes were identified (12 each among clones collected on SLV-2 and Kubanskoe krasnoe 1677, and 10 on Efremovskoe below). The phenotype that was avirulent to all barley accessions dominated (Table 3). Two virulence phenotypes (10 and 14) were noted only among the collections from Kubanskoe krasnoe 1677, and phenotype 7 was unique for the SLV-2 accession.

Table 4. Segregation for resistance to *S. graminum* of F₂ hybrids from crossing resistant barley accessions with a susceptible tester

Cross combination	Total number of plants	The ratio of phenotypes R : S		χ^2	<i>p</i>
		observed	expected		
k-3885 × Belogorskiy	125	93 : 32	3 : 1	0.024	0.8–0.9
k-3904 × Belogorskiy	207	147 : 60	3 : 1	1.754	0.1–0.2
k-04080 × Belogorskiy	294	225 : 69	3 : 1	0.367	0.5–0.75

Note. $\chi^2_{0,05} = 3,84$. R — resistance, S — susceptibility.

Greenbug clones with different virulence phenotypes (“test clones”) enable the identification of resistance genes in isolated barley forms. If at least one clone that is avirulent to the tester of a given resistance gene damages the variety under study, this means that the variety does not have a functional allele of this gene. When the experimental accessions were infested with *S. graminum* with virulence phenotype 2, the Post variety was found to be susceptible, while the accessions from Mongolia were resistant to the pest. This means that accessions k-3904, k-4080, and k388 have resistance gene alleles that differ from the previously identified *Rsg1* gene. Comparison of the interaction of experimental accessions with aphids with virulence phenotypes 3, 4, and 5 indicated a difference in the genetic control of the trait in all landraces from Mongolia. These conclusions were supported by a pairwise comparison of the resistance of the accessions to aphids with virulence phenotypes 6–14.

In the analysis of the F₂ hybrids, the damage to lines isolated from accessions k-3904, k-4080, and k3885 varied between 1 and 5 points. In the F₁ hybrid, k-4080 × Belogorskiy, resistance dominated, with a plant damage score of 2–3 points. In two other cases, the level of resistance of heterozygotes was somewhat lower (2–7 points), indicating incomplete dominance of the trait. In the F₂ populations, the resulting phenotype ratio corresponded to the theoretically expected 3R:1S (Table 4), indicating that barley landraces from Mongolia carry by one dominant resistance gene.

CONCLUSION

The genetic diversity of barley accessions from Mongolia in terms of resistance to the greenbug is low.

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Six heterogeneous accessions were identified, in which plants with high resistance to the pest were detected. Among 28 accessions, damage to the leaf surface of the resistant component varied from 31% to 60%. As a result of assessment of the resistance of pure lines selected from the heterogeneous accessions, k-3885, k-3904, and k-4080, as well as the Post variety (carrier of the previously identified *Rsg1* gene) to 86 aphid clones, 15 virulence phenotypes were identified. Accessions k-3885, k-3904, and k-4080 each have one dominant resistance allele, which differ from each other and also differ from *Rsg1*. *S. graminum* genotypes were revealed to interact differentially not only with the main genes but also with weakly expressed resistance genes of barley lines.

ADDITIONAL INFORMATION

Author contribution. Thereby, all authors made equal contribution to the conception of the work, acquisition, analysis, interpretation of data for the work, drafting and revising the work, final approval of the version to be published and agree to be accountable for all aspects of the work. Contribution of each author: E.E. Radchenko — concept and design of the study, analysis of the data obtained, writing the text; R.A. Abdullaev — analysis of the data obtained, writing the text; D.E. Akimova — collection and processing of materials, writing text, literature review; I.Yu. Zaitseva — collection and processing of materials, writing text.

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AUTHORS' INFO

***Evgeny E. Radchenko**, Dr. Sci. (Biol.),
Main Research Associate; address: 42, 44, Bolshaya Morskaya st.,
Saint Petersburg, 190000, Russia;
ORCID: <https://orcid.org/0000-0002-3019-0306>;
eLibrary SPIN: 1667-0530; Scopus: 7005353107;
e-mail: eugene_radchenko@rambler.ru

Renat A. Abdullaev,
Cand. Sci. (Biol.), Senior Research Associate;
ORCID: <https://orcid.org/0000-0003-1021-7951>;
Scopus: 57211915135; e-mail: abdullaev.1988@list.ru

Daria E. Akimova, Postgraduate Student;
ORCID: <https://orcid.org/0000-0002-0657-1715>;
e-mail: nezabutkabitter@yandex.ru

Irina Yu. Zajtseva, Student;
ORCID: <https://orcid.org/0000-0001-8283-9747>;
e-mail: irzajtseva@yandex.ru

ОБ АВТОРАХ

***Евгений Евгеньевич Радченко**, д-р биол. наук,
гл. научн. сотр.; адрес: Россия, 190000, Санкт-Петербург,
ул. Большая Морская, д. 42, 44;
ORCID: <https://orcid.org/0000-0002-3019-0306>;
eLibrary SPIN: 1667-0530; Scopus: 7005353107;
e-mail: eugene_radchenko@rambler.ru

Ренат Абдуллаевич Абдуллаев,
канд. биол. наук, ст. научн. сотр.;
ORCID: <https://orcid.org/0000-0003-1021-7951>;
Scopus: 57211915135; e-mail: abdullaev.1988@list.ru

Дарья Евгеньевна Акимова, аспирант;
ORCID: <https://orcid.org/0000-0002-0657-1715>;
e-mail: nezabutkabitter@yandex.ru

Ирина Юрьевна Зайцева, студентка;
ORCID: <https://orcid.org/0000-0001-8283-9747>;
e-mail: irzajtseva@yandex.ru

* Corresponding author / Автор, ответственный за переписку