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Disease resistance in the genus *Aegilops* L. – stem rust, leaf rust, stripe rust, and powdery mildew

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Summary

Resistance of the Gatersleben *Aegilops* collection was studied in relation to the following wheat diseases: stem rust *(Puccinia graminis)*, leaf rust *(Puccinia recondita)*, stripe rust *(Puccinia striiformis)* and powdery mildew *(Erysiphe graminis)*. Numerous sources of complete, combined or single resistance have been detected in 487 accessions of 21 *Aegilops* species. Potential donors of the complete resistance have been found in diploid *Ae. speltoides*, *Ae. longissima* ssp. *sharonensis*, *Ae. markgrafii* and tetraploid *Ae. geniculata*. Methods of a transfer of resistance genes from particular *Aegilops* species to the common wheat, *Triticum aestivum*, are discussed.

1. Introduction

Breeding of field crops for disease resistance has become a powerful tool of modern agriculture in the struggle with plant pathogens. Unfortunately, the resistance is of limited duration, because biotypes of pathogens with new virulence will appear earlier or later when a new resistant variety is being grown on a large scale. Therefore, a continuous search for new effective resistance genes is made in the gene pool of cultivated species for their use in plant breeding. Genetic resources within the species may be rather limited or already exhausted in respect of resistance against certain pathogens so that the search must be carried out in related species or genera. A similar situation is in the common wheat, *Triticum aestivum* L., especially in relation to leaf rust and powdery mildew. Our increasing knowledge of cytogenetic relations within the subtribe Triticinae and new crossing techniques with the use of embryo cultures allow a broader employment of related species in distant hybridization with wheat and make the transfer of desirable genes feasible.

A large genetic reservoir of economically important traits is in the genus *Aegilops* L. which is closely related to *Triticum*, because at least one of the three genomes of *Triticum aestivum* comes from *Aegilops*. Some authors unite the two genera on the basis of their cytogenetic similarity (Bowden 1959, Morris and Sears 1967). In the present paper we maintain *Aegilops* as a separate genus following the argumentation of Hammer (1980a and b).

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Resistance of *Aegilops* species to wheat diseases has been studied by several authors. As early as in 1918 VAVILOV found high resistance of *Ae. geniculata* and *Ae. triuncialis* to stem and leaf rusts and powdery mildew (VAVILOV 1964). A summary of earlier studies related to the resistance of *Aegilops* species to diseases was made by BELL and LUPTON (1955); more recent papers were reviewed by HAMMER (1980b). It is comprehensible that resistance characteristics of the *Aegilops* species are sometimes inconsistent, because different pathogen isolates and different host genotypes have been used by various authors. Obviously, the *Aegilops* species are internally differentiated in their disease resistance. Nevertheless, some of them are characterized as a whole by a higher resistance to respective pathogens.

Ae. speltoides, Ae. markgrafii, Ae. geniculata, Ae. uniaristata, and *Ae. comosa* have been reported as the most resistant species to wheat stem rust (BELL and LUPTON 1955, HIRATSUKA 1954, PANAJOTOV and TODOROV 1979, PASQUINI 1980).

Considerable levels of resistance to wheat leaf rust has been found in *Ae. speltoides, Ae. markgrafii,* and *Ae. comosa* (BELL and LUPTON 1955, HIRATSUKA 1955, MIGUŠOVA and GRIGOR'EVA 1973, PANAJOTOV and TODOROV 1979, PASQUINI 1980).

Stripe rust resistance has not been studied so often as resistance to the abovementioned pathogens. HASSEBRAUK (1931 – cit. BELL and LUPTON 1955) considered *Ae. cylindrica* and *Ae. geniculata* as resistant to the physiologic race 4. HIRATSUKA (1954) working with a limited number of accessions (1 to 3 from each species) found *Ae. speltoides, Ae. uniaristata* and *Ae. triuncialis* to be resistant. BELL and LUPTON (1955) detected resistance to stripe rust in some accessions of *Ae. speltoides, Ae. markgrafii* and *Ae. geniculata.*

The whole genus *Aegilops* is characterized by high resistance to powdery mildew of wheat (BELL and LUPTON 1955, ZITELLI 1980). PANAJOTOV and TODOROV (1979), PASQUINI (1980) and MIGUŠOVA et al. (1980) reported differential reaction to this disease in some species but all species contained also resistant lines.

From the pratical point of view it is important that some resistances of *Aegilops* spp. have been already transferred to hexaploid wheat. SEARS (1956) was the first who succeeded in this direction with the transfer of leaf rust resistance from *Ae. umbellulata* (Lr 9). Genes for resistance to the same pathogen were also transferred from *Ae. tauschii* (Lr 21 and Lr 22 – KERBER and DYCK 1969, DYCK and KERBER 1970), *Ae. speltoides* (DVOŘÁK 1977, DVOŘÁK and KNOTT 1980 – two unnamed genes; MCINTOSH et al. 1982 – Lr 28). The genes Sr 32, Sr 33 and Sr 34 conditioning resistance to wheat stem rust were derived from *Ae. speltoides, Ae. tauschii,* and *Ae. comosa,* respectively (SEARS, unpubl. – cit. DVOŘÁK and KNOTT 1980, KERBER and DYCK 1978, MCINTOSH et al. 1982). *Ae. comosa* was also the donor of a gene for resistance to stripe rust (Yr 8 – RILEY et al. 1968). These first positive results indicate further possibilities for the use of the genus *Aegilops* as a donor of disease resistance genes in distant hybridization with wheat.

It is necessary to stress the fact that various *Aegilops* species are related to wheat in different degree. Thus, transfer of economically important traits will be in certain cases easier, in other ones more difficult.

According to the classification of wild gene pools in the Triticinae made by FELDMAN (1979) on the basis of their phylogenetic and cytogenetic relationships with the cultivated common wheat, *Aegilops* species fall into the following groups:

I – Species with homologous genomes
  1) diploid donor of the D genome
    Ae. tauschii
  2) polyploids sharing the D genome
    Ae. crassa, Ae. ventricosa, Ae. cylindrica, Ae. juvenalis

II –Species with homoeologous genomes
  1) closely related species (those containing the S genome)
    Ae. searsii, Ae. longissima, Ae. bicornis, Ae. speltoides, Ae. peregrina, Ae. kotschyi
  2) less closely related species
    Ae. mutica, Ae. markgrafii, Ae. comosa, Ae. uniaristata, Ae. umbellulata, Ae. geniculata, Ae. neglecta, Ae. lorentii, Ae. columnaris, Ae. triuncialis.

The main difference between the subgroups II/1 and II/2 is that in the former the absence of a weak pairing suppressor (as that located on the chromosome 3 D in hexaploid wheat) or the use of intermediate pairing genotypes of S genome diploids are sufficient for the induction of preferential homoeologous pairing of the S genome chromosomes with those of the B genome of wheat (SEARS 1982). In this way the undesirable homoeologous pairing between A and D wheat genome chromosomes is limited and this can be utilized in gene transfers from the S genome species to wheat.

In the subgroup II/2, the less closely related species, the absence of the strong suppressor of homoeologous pairing which is located on the 5 B chromosome of polyploid wheats or the use of high pairing genotypes of *Ae. speltoides* or *Ae. mutica* are necessary for the induction of homoeologous pairing in their hybrids with polyploid wheats.

In the present paper the above-mentioned grouping of *Aegilops* species is used in the compilation of tables and in the discussion of results because it has practical implications for the selection of appropriate methods of gene transfer from the particular *Aegilops* species to wheat; for details see FELDMAN (1979), FELDMAN and SEARS (1981).

The main aim of our work was to contribute to the better knowledge of disease resistance in the genus *Aegilops*, to detect donors of the resistance in the Gatersleben collection (see also FRAUENSTEIN and HAMMER 1985) and to indicate ways of their employment in wheat breeding.

2. Material and methods

The object of our study was the *Aegilops* collection maintained in the Zentralinstitut für Genetik und Kulturpflanzenforschung, Gatersleben (GDR). The authors wish to thank Dr. CHR. O. LEHMANN, Head of the Genebank, Gatersleben, for his kind cooperation. The numbers of investigated accessions of each species are listed in Table 1 and compared with the collected world gene pool of some *Aegilops* species in Table 2.

For this comparison the data of CROSTON and WILLIAMS (1981) were used and it can be concluded that the studied collection represents a considerable part of the collected world gene pool in some species. More details about the Gatersleben collection were published elsewhere (HAMMER 1980 b).

All the tests of resistance were carried out in the Research Institute of Crop Production in Prague – Ruzyně (Czechoslovakia) during the period 1980–1982.

Table 1

The classification of the genus *Aegilops* (HAMMER 1980 b) with numbers of accessions studied (*n*) and genomes formulae

	n	Ploidy level		
		2x	4x	6x
subg. *Amblyopyrum* Jaub. et Sp.				
Ae. mutica Boiss.	3	Mt		
subg. *Sitopsis* Jaub. et Sp.				
Ae. speltoides Tausch	53	S		
Ae. longissima Schweinf. et Muschl. emend. Eig.				
ssp. *longissima*	16	S^l		
ssp. *sharonensis* (Eig) Hammer	16	S^1		
Ae. bicornis (Forssk.) Jaub. et Sp.	3	S^b		
Ae. searsii Feldman et Kislev ex Hammer	3	S^s		
subg. *Aegilops*				
sect. *Cylindropyrum* (Jaub. et Sp.) Zhuk. emend. Kihara				
Ae. markgrafii (Greuter) Hammer	5	C		
Ae. cylindrica Host	26		CD	
sect. *Vertebrata* Zhuk. emend. Kihara				
Ae. tauschii Coss.	132	D		
Ae. crassa Boiss.	23		D M^{cr}	D D_2M^{cr} or DM^{cr} S^l
Ae. ventricosa Tausch	14		DM^v	
Ae. juvenalis (Thell.) Eig	7			DM^{cr} C^u
sect. *Compyrum* (Jaub. et Sp.) Zhuk. emend. Kihara				
Ae. comosa Sibth. et Sm.	3	M		
Ae. uniaristata Vis.	4	M^u		
sect. *Aegilops*				
Ae. umbellulata Zhuk.	7	C^u		
Ae. peregrina (Hackel) Maire et Weiller	10		$C^u S^v$	
Ae. kotschyi Boiss.	5		C^uS^v	
Ae. triuncialis L.	54		C^uC	
Ae. lorentii Host	9		C^uM^b	
Ae. columnaris Zhuk.	9		C^uM^c	
Ae. neglecta Req. ex Bertol.	22		C^uM^t	$C^uM^tM^{t2}$
Ae. geniculata Roth.	63		C^uM^o	
Total	487			

Table 2

Species in which more than 20 % of the world collected gene pool (cf. CROSTON and WILLIAMS 1981) was investigated

Species	Accessions in world gene pool (w. g. p.)	Accessions investigated (invest.)	Percentage invest. (w. g. p.) %
Ae. longissima	57	32	56,1
Ae. uniaristata	8	4	50,0
Ae. ventricosa	29 (with dupl.)	14	48,3
Ae. geniculata	182	63	34,6
Ae. tauschii	501	132	26,3
Ae. crassa	90	23	25,6
Ae. juvenalis	30	7	23,3
genus *Aegilops* (total)	4069	487	12,0

Reaction to the following pathogens was studied:
wheat stem rust (*Puccinia graminis* f. sp. *tritici* Erikss. et Henn.)
wheat leaf rust (*Puccinia recondita* Rob. ex Desm.)
wheat stripe rust (*Puccinia striiformis* West)
powdery mildew of wheat (*Erysiphe graminis* DC. f. sp. *tritici* Marchal)

2.1. *Tests of stem rust resistance*

For seedling resistance tests the plants were grown in pots in the open air (May, 1980) and in the two leaf-stage the first leaves were inoculated with a mixture of uredospores of isolates 69, 334 and 802 belonging to physiologic races 21, 34 and 11, respectively.

Adult plant resistance was investigated in field infection nurseries in the tests repeated in three successive years (1980, 1981, 1982) using the pathogen isolate G 425 belonging to the race 11. Both seedling and adult plant resistances were evaluated according to the scale of STAKMAN et al. (1962) based on infection types. Differences in intensity of infection (percentage of leaf area attacked) were not scored because this character is difficult to assess in *Aegilops* species with regard to their dissimilarity in leaf size and structure. Moreover, the resistance expressed by infection types seems to be more suitable for transfer purposes in distant hybridization, because screening for a clearly-defined qualitative trait in a hybrid progeny is much easier and this type of resistance usually is simply inherited as the successful alien transfers have proved (see Introduction).

2.2. *Tests of leaf rust resistance*

The climatic conditions in the period 1980–1982 were not suitable for the development of sufficiently intensive artificial leaf rust infection in the field nurseries, thus only seedling resistance in the greenhouse was evaluated. In three successive tests the entire *Aegilops* collection was inoculated with single isolates of physiological races UN 10–14, UN 13–77 and UN 3–61, respectively. The mode of evaluation was identical with that in the stem rust.

2.3. *Tests of stripe rust resistance*

Seedling resistance was studied in the same test as described earlier for stem rust (see Part. 2.1.) using second leaves for inoculation with stripe rust race 3/55 (Test A).

Every year (1980, 1981 and 1982), stripe rust infection nurseries for adult plant resistance studies were established in Prague and a mixture of 10 isolates (Test B), an isolate of the race 33 E 128 (Test C) and an isolate from cv. Purdue (Test D) were used for inoculation in the respective years. An additional infection nursery located at the Agricultural Research Station in Klatovy (1982) provided data on adult plant resistance in relation to an isolate from locality Trutnov (Test E).

A four grade scale based on infection types (VALKOUN et al. 1982) was used for evaluation in every stripe rust resistance test.

2.4. *Tests of powdery mildew resistance*

The severe natural infection with powdery mildew of wheat was utilized for assessment of adult plant resistance both in Prague and Klatovy field nurseries in 1982. The evaluation of resistance was made according to our own scale (VALKOUN et al. 1982).

2.5. *Determination of the resistance level in Aegilops accessions and species*

It follows from 2.1. to 2.4. that maximum number of disease scores in each *Aegilops* accession was four in stem rust, three in leaf rust, five in stripe rust, two in powdery mildew. The level of resistance to individual diseases in each *Aegilops* accession was determined on the basis of the disease score pattern, when the highest ("the worst") score was decisive for classification according to the Table 3 (without regarding the growth stage).

Table 3

Disease score

Category	the highest disease score (x)	
	rusts	mildew
R – resistant	$x \leqq 1$	$x = 0$
MR – moderarely resistant	$1 < x \leqq 2$	$0 < x \leqq 2$
S – susceptible	$x > 2$	$x > 2$

The sum of the final resistance characteristics of all accessions belonging to the same species then gave the total resistance pattern of the species in relation to the respective pathogens which was expressed in percentages of the R, MR and S categories (Tables 4, 5, 7 and 9).

In leaf and stripe rusts, where results of more tests with various pathogen isolates were at disposal, a subcategory of partially resistant (PR) accessions was established within the subsceptible (S) category, i.e., these accessions remained in some tests resistant but in the others were susceptible. The PR categories are further analyzed in Tables 6 and 8, where the reaction rates expressed as the proportion of the number of resistant and susceptible accessions in the particular tests and percentages of the resistant accessions of the total number are shown for each *Aegilops* species and also for the whole genus. The latter data characterize virulence of the pathogen isolates employed in the tests.

3. Results

3.1. *Resistance to stem rust (P. graminis)*

The total characteristic of the genus *Aegilops* in respect to this pathogen is presented in Table 4. The total percentages 18,6 resistant, 6,0 moderately resistant and 74,5 susceptible demonstrate that the genus shows the lowest resistance to this disease from all the four investigated pathogens in spite of that only a single

Table 4

Resistance to stem rust

Species	*n*	R		MR		S		RS*	
		n	%	*n*	%	*n*	%	*n*	%
Ae. tauschii	130	15	11,5	7	5,4	108	81,5	–	–
Ae. crassa	22	–	–	–	–	22	100,0	–	–
Ae. ventricosa	13	–	–	–	–	13	100,0	–	–
Ae. cylindrica	25	–	–	–	–	25	100,0	–	–
Ae. juvenalis	6	–	–	–	–	6	100,0	–	–
Ae. searsii	3	–	–	–	–	3	100,0	–	–
Ae. longissima									
ssp. *longissima*	15	–	–	–	–	15	100,0	–	–
ssp. *sharonensis*	16	2	12,5	–	–	13	81,2	1	6,3
Ae. bicornis	3	–	–	–	–	3	100,0	–	–
Ae. speltoides	52	42	80,8	4	7,7	3	5,8	3	5,8
Ae. peregrina	9	–	–	–	–	9	100,0	–	–
Ae. kotschyi	5	–	–	–	–	5	100,0	–	–
Ae. mutica	3	–	–	–	–	3	100,0	–	–
Ae. markgrafii	5	3	60,0	–	–	2	40,0	–	–
Ae. comosa	3	–	–	1	33,3	2	66,6	–	–
Ae. uniaristata	4	1	25,0	3	75,0	–	–	–	–
Ae. umbellulata	6	–	–	–	–	6	100,0	–	–
Ae. geniculata	57	21	36,8	10	17,5	26	45,6	–	–
Ae. neglecta	22	3	13,6	2	9,1	17	77,3	–	–
Ae. lorentii	9	–	–	–	–	9	100,0	–	–
Ae. columnaris	8	–	–	–	–	8	100,0	–	–
Ae. triuncialis	54	–	–	1	1,9	53	98,1	–	–
genus *Aegilops* (total)	467	87	18,6	28	6,0	348	74,1	4	0,9

* heterogenous accessions

isolate of the pathogen was used for the adult plant resistance tests. From the species with homologous genomes only some accessions of *Aegilops tauschii* were resistant.

3.1.1. Species with homoeologous genomes

Closely related species

This group includes *Ae. speltoides*, the most resistant *Aegilops* species at all (80,8 % of accessions resistant and 7,7 % moderately resistant). Two resistant accessions were found in *Ae. longissima* ssp. *sharonensis*.

Less closely related species

Ae. markgrafii is the most resistant representative of this group with 60,0 % of resistant entries, but only few accessions (5) have been studied.

Among other diploids *Ae. uniaristata* is characterized by a high level of resistance because all its accessions belong to the categories R or MR; *Ae. comosa* had one moderately resistant accession. In the polyploids the resistance was found only in *Ae. geniculata* and *Ae. neglecta* with 36,8 and 13,6 % of resistant entries, respectively. One MR accession appeared in *Ae. triuncialis*.

3.2. *Resistance to leaf rust (P. recondita)*

As explained in the previous chapter (Material and methods), this resistance was tested only in seedlings. The total resistance pattern in the genus *Aegilops* was 24,6 % of resistant, 12,8 % moderately resistant and 58,3 % of susceptible accessions (see Tab. 5).

Table 5

Resistance to leaf rust

Species						S				RS*	
	n	R		MR		total		PR			
		n	%	*n*	%	*n*	%	*n*	%	*n*	%
Ae. tauschii	126	10	7,9	5	4,0	110	87,3	38	30,2	1	0,8
Ae. crassa	22	–	–	–	–	22	100,0	–	–	–	–
Ae. ventricosa	13	–	–	–	–	13	100,0	6	46,2	–	–
Ae. cylindrica	26	3	11,5	3	11,5	17	65,4	3	11,5	3	11,5
Ae. juvenalis	6	–	–	–	–	6	100,0	–	–	–	–
Ae. searsii	3	2	66,6	–	–	1	33,3	1	33,3	–	–
Ae. longissima											
ssp. *longissima*	16	4	25,0	1	6,3	8	50,0	7	43,8	3	18,8
ssp. *sharonensis*	16	2	12,5	2	12,5	10	62,5	8	50,0	2	12,5
Ae. bicornis	3	–	–	–	–	3	100,0	–	–	–	–
Ae. speltoides	52	47	90,4	1	1,9	3	5,8	2	3,8	1	1,9
Ae. peregrina	10	6	60,0	3	30,0	–	–	–	–	1	10,0
Ae. kotschyi	5	1	20,0	1	20,0	3	60,0	1	20,0	–	–
Ae. mutica	2	–	–	–	–	2	100,0	2	100,0	–	–
Ae. markgrafii	5	4	80,0	–	–	1	20,0	–	–	–	–
Ae. comosa	2	1	50,0	–	–	1	50,0	1	50,0	–	–
Ae. uniaristata	4	–	–	–	–	4	100,0	1	25,0	–	–
Ae. umbellulata	8	6	75,0	–	–	2	25,0	1	12,5	–	–
Ae. geniculata	58	7	12,1	14	24,1	32	55,2	23	39,7	5	8,6
Ae. neglecta	22	–	–	3	13,6	17	77,3	8	36,4	2	9,1
Ae. lorentii	9	5	55,6	3	33,3	1	11,1	–	–	–	–
Ae. columnaris	7	4	57,1	2	28,6	1	14,3	1	14,3	–	–
Ae. triuncialis	51	13	25,5	21	41,2	15	29,4	13	25,5	2	3,9
genus *Aegilops* (total)	468	115	24,6	60	12,8	273	58,3	116	24,8	20	4,3

* heterogenous accessions

3.2.1. *Species with homologous genomes*

The most resistant species of the group, *Ae. cylindrica*, possessed 11,5 % and the D genome donor, *Ae. tauschii*, 7,9 % of resistant entries. Both species and *Ae. ventricosa* included also some partially resistant accessions, the other species proved to be completely susceptible.

3.2.2. Species with homolologous genomes

Closely related species

Ae. speltoides is with 90,4 % of resistant accessions the most resistant species not only in this group but in the entire genus *Aegilops* as well. A high level of resistance was found in *Ae. peregrina.* With the exception of *Ae. bicornis* resistant entries were discovered in all the other diploids and tetraploids.

Less closely related species

Similarly as in the stem rust *Ae. markgrafii* showed the highest resistance (80,0 % of resistant accessions), followed by *Ae. umbellulata* (75,0 %), *Ae. columnaris* (57,1 %) and *Ae. lorentii* (55,6 %).

3.2.3. Reaction rates in the partially resistant (PR) category

The reaction rates (R : S) for the *Aegilops* species with partially resistant accessions and percentages of the resistant reactions are presented in Table 6. From the data it is concluded that the isolate of the physiologic race UN 3–61 is the most pathogenic biotype of wheat leaf rust in relation to the given *Aegilops* collection (only 20,5 % of resistant reactions), whereas the isolate belonging to the race UN 13–77 remains the least virulent in this respect (69,0 % of resistant reactions).

Table 6

Reaction rates in the partially resistant category (PR) to leaf rust

Species	UN 10–14		UN 13–77		UN 3–61	
	R : S	% R	R : S	% R	R : S	% R
Ae. tauschii	2/24	7,7	34/4	89,5	8/27	22,9
Ae. ventricosa	3/0	100,0	3/3	50,0	0/5	0
Ae. cylindrica	1/0	100,0	2/1	66,7	0/3	0
Ae. searsii	0/1	0	1/0	100,0	0/1	0
Ae. longissima						
ssp. *longissima*	5/0	100,0	3/3	50,0	0/5	0
ssp. *sharonensis*	5/3	62,5	4/4	50,0	3/5	37,5
Ae. speltoides	1/0	100,0	0/2	0	1/1	50,0
Ae. kotschyi	0/1	0	1/0	100,0	0/1	0
Ae. mutica	1/1	50,0	1/1	50,0	1/1	50,0
Ae. comosa	–	–	1/0	100,0	0/1	0
Ae. uniaristata	1/0	100,0	0/1	0	0/1	0
Ae. umbellulata	–	–	1/0	100,0	0/1	0
Ae. geniculata	12/0	100,0	17/0	70,8	3/21	12,5
Ae. neglecta	6/0	100,0	1/7	12,5	4/4	50,0
Ae. lorentii	–	–	0/1	0	1/0	100,0
Ae. columnaris	1/0	100,0	0/1	0	0/1	0
Ae. triuncialis	6/3	66,7	12/1	92,3	2/11	15,4
genus *Aegilops* (total)	44/33	57,1	80/36	69,0	23/89	20,5

Pathogenicity of the isolates seems to be species-specific, if this is true the term "virulence" could be used instead of "pathogenicity". For instance, UN 13–77 is the most virulent race for *Ae. neglecta* but almost avirulent for *Ae. tauschii,* while the reverse situation occurs with UN 10–14.

On the basis of the FLOR's gene-for-gene hypothesis (FLOR 1955) it is concluded that this specific reaction pattern within the genus *Aegilops* indicates presence of resistance genes which are race-specific to the wheat leaf rust.

3.3. Resistance to stripe rust (P. striiformis)

This resistance has been studied most thoroughly, in five tests in total. Resistance to stripe rust seems to be more widespread in the genus *Aegilops* than the resistances to other cereal rusts. The total characteristic (33,3 % of resistant, 9,6 % moderately resistant and 57,1 % of susceptible accessions) is shown in Tab. 7.

Table 7

Resistance to stripe rust

Species	*n*	R		MR		S			
						total		PR	
		n	%	*n*	%	*n*	%	*n*	%
Ae. tauschii	132	10	7,6	10	7,6	112	84,8	66	50,0
Ae. crassa	23	–	–	–	–	23	100,0	4	17,4
Ae. ventricosa	13	6	46,2	2	15,4	5	38,5	5	38,5
Ae. cylindrica	25	–	–	–	–	25	100,0	6	24,0
Ae. juvenalis	6	–	–	–	–	6	100,0	6	100,0
Ae. searsii	3	1	33,3	–	–	2	66,7	–	–
Ae. longissima									
ssp. *longissima*	14	4	28,6	3	21,4	7	50,0	7	50,0
ssp. *sharonensis*	16	3	18,8	–	–	13	81,2	7	43,2
Ae. bicornis	3	–	–	–	–	3	100,0	2	66,7
Ae. speltoides	52	43	82,7	3	5,8	6	11,5	6	11,5
Ae. peregrina	9	3	33,3	1	11,1	5	55,6	3	33,3
Ae. kotschyi	5	1	20,0	1	20,0	3	60,0	–	–
Ae. mutica	3	1	33,3	1	33,3	1	33,3	1	33,3
Ae. markgrafii	5	4	80,0	–	–	1	20,0	1	20,0
Ae. comosa	3	3	100,0	–	–	–	–	–	–
Ae. uniaristata	4	3	75,0	1	25,0	–	–	–	–
Ae. umbellulata	7	2	28,6	–	–	5	71,4	3	42,9
Ae. geniculata	62	32	51,6	8	12,9	22	35,5	20	32,3
Ae. neglecta	22	18	81,8	2	9,1	2	9,1	2	9,1
Ae. lorentii	8	4	50,0	1	12,5	3	37,5	3	37,5
Ae. columnaris	9	2	22,2	2	22,2	5	55,6	4	44,4
Ae. triuncialis	54	19	35,2	11	20,4	24	44,0	23	42,6
genus *Aegilops* (total)	478	159	33,3	46	9,6	273	57,1	169	35,4

3.3.1. Species with homologous genomes

Tetraploid *Ae. ventricosa* had almost a half of the accessions resistant to this pathogen. Resistant entries were found in low frequency (7,6 %) in the D genome donor, *Ae. tauschii*. The remaining species were susceptible.

3.3.2. *Species with homoeologous genomes*

Closely related species

Diploid *Ae. speltoides* is again the most resistant of this group with 82,7 % of resistant accessions. Resistant genotypes were also found in both subspecies of *Ae. longissima*, in *Ae. searsii* and tetraploid *Ae. peregrina* and *Ae. kotschyi*, while *Ae. bicornis* proved to be susceptible.

Less closely related species

The group as a whole is relatively resistant, all species have at least 20 % of resistant accessions. *Ae. comosa* resulted in the most resistant species of the genus having 100 % of resistant entries but only three accessions were tested in total. *Ae. neglecta* (81,8 %), *Ae. markgrafii* (80,0 %), *Ae. uniaristata* (75,0 %) and *Ae. geniculata* (51,6 %) are the other species with remarkable stripe rust resistance.

3.3.3. *Reaction rates in the partially resistant (PR) category*

Similarly as in the leaf rust the reaction rates for the species with partially resistant accessions are summarized in Table 8. The test B, where a mixture of 10 isolates was used as the inoculum, proved to be the most appropriate for screening

Table 8

Reaction rates in the partially resistant category (PR) to stripe rust

Tests*	A		B		C		D		E	
Species	R : S	% R	R : S	% R	R : S	% R	R : S	% R	R : S	% R
Ae. tauschii	15/41	26,8	16/45	26,2	30/36	45,5	24/11	68,6	32/32	50,0
Ae. crassa	2/2	50,0	0/4	0	0/4	0	1/2	33,3	2/2	50,0
Ae. ventricosa	1/2	33,3	2/2	50,0	5/0	100,0	3/1	75,0	4/1	80,0
Ae. cylindrica	2/4	33,3	3/3	50,0	2/4	33,3	3/3	50,0	1/5	16,7
Ae. juvenalis	3/2	60,0	1/5	16,7	3/3	50,0	0/4	0	1/5	16,7
Ae. longissima										
ssp. *longissima*	5/1	83,3	3/4	42,9	5/1	83,3	1/4	20,0	4/1	80,0
ssp. *sharonensis*	4/3	57,1	5/2	71,4	1/3	25,0	1/2	33,3	2/2	50,0
Ae. bicornis	0/2	0	2/0	100,0	0/2	0	0/2	0	0/1	0
Ae. speltoides	4/2	66,7	5/1	83,3	3/3	50,0	4/1	80,0	4/1	80,0
Ae. peregrina	3/0	100,0	1/2	33,3	1/2	33,3	2/1	66,7	0/3	0
Ae. mutica	–	–	1/0	100,0	0/1	0	–	–	0/1	0
Ae. markgrafii	–	–	1/0	100,0	0/1	–	0/1	0	0/1	0
Ae. umbellulata	1/2	33,3	0/3	0	1/2	33,3	3/0	100,0	2/0	100,0
Ae. geniculata	14,5	73,7	6/14	30,0	19/1	95,0	9/6	60,0	17/1	94,4
Ae. neglecta	0/2	0	2/0	100,0	2/0	100,0	2/0	100,0	1/1	50,0
Ae. lorentii	1/2	33,7	3/0	100,0	3/0	100,0	2/0	100,0	1/2	33,0
Ae. columnaris	4/0	100,0	2/2	50,0	2/2	50,0	1/3	25,0	1/3	25,0
Ae. triuncialis	13/10	56,5	14,9	60,9	17/6	73,9	10/11	47,6	18/4	81,8
genus *Aegilops* (total)	72/80	47,4	67/96	41,1	94/71	57,0	66/52	55,9	90/66	57,7

* for explanation see Part. 2.3

purposes having only 41,1 % of resistant reactions. Differential reactions in tests with single isolates (tests A, C, D and E) suggest a presence of the race-specific resistance genes to stripe rust.

3.4. *Resistance to powdery mildew (E. graminis)*

The determination of powdery mildew resistance was based on the evaluation of a strong natural infection of adult plants in two localities. The results in Tab. 9 indicate that the genus *Aegilops* is a good genetic resource of resistance to this disease with about two thirds of resistant accessions.

Table 9

Resistance to powdery mildew

Species	*n*	R		MR		S	
		n	%	*n*	%	*n*	%
Ae. tauschii	114	31	27,2	12	10,5	71	62,3
Ae. crassa	22	2	9,1	–	–	20	90,9
Ae. ventricosa	12	11	91,7	–	–	1	8,3
Ae. cylindrica	27	15	55,6	3	11,1	9	33,3
Ae. juvenalis	6	4	66,7	–	–	2	33,3
*Ae. searsii**	–	–	–	–	–	–	–
Ae. longissima							
ssp. *longissima*	7	6	85,7	–	–	1	14,3
ssp. *sharonensis*	12	12	100,0	–	–	–	–
Ae. bicornis	2	1	50,0	–	–	1	50,0
Ae. speltoides	50	39	78,0	1	2,0	10	20,0
Ae. peregrina	9	8	88,9	–	–	1	11,1
Ae. kotschyi	4	4	100,0	–	–	–	–
Ae. mutica	2	2	100,0	–	–	–	–
Ae. markgrafii	5	4	80,0	–	–	1	20,0
Ae. comosa	1	–	–	–	–	1	100,0
Ae. uniaristata	4	–	–	–	–	4	100,0
Ae. umbellulata	6	4	66,7	–	–	2	33,3
Ae. geniculata	57	52	91,2	3	5,3	2	3,5
Ae. neglecta	22	21	95,5	–	–	1	4,5
Ae. lorentii	7	7	100,0	–	–	–	–
Ae. columnaris	7	6	85,7	–	–	1	14,3
Ae. triuncialis	51	45	88,2	2	3,9	4	7,8
genus *Aegilops* (total)	427	274	64,2	21	4,9	132	30,9

* not tested

3.4.1. *Species with homologous genomes*

The most resistant species is *Ae. ventricosa* with 91,7 % of resistant accessions. Surprisingly enough, the tests revealed good resistance in hexaploid *Ae. juvenalis*, whereas *Ae. crassa* was the most susceptible *Aegilops* species at all. *Ae. tauschii*, the D genome donor, possesses also some sources of resistance (27,2 %).

3.4.2. *Species with homoeologous genomes*

Closely related species

The whole group shows a considerable level of resistance. Diploid *Ae. longissima* ssp. *sharonensis* and tetraploid *Ae. kotschyi* remained completely resistant.

Less closely related species

With the exception of the susceptible section *Comopyrum* these species are characterized with high resistance (80–100 % of resistant accessions), only *Ae. umbellulata* is somewhat more susceptible.

3.5. *Resistance pattern of the Aegilops species*

The characteristics of disease resistance in the *Aegilops* spp. expressed as percentages of resistant accessions are shown in Table 10 and graphically demonstrated in Figure 1. The total level of resistance of the whole genus *Aegilops* to the particular diseases is summarized in the last line of Table 10 and in the final diagramme of Fig. 1. This level gradually increases from stem rust (18,6 %), leaf rust (24,6 %), stripe rust (33,3 %) up to 64,2 % of resistant accessions in powdery mildew.

Table 10

Resistance pattern in the *Aegilops* species

Species	% R accessions			
	P. graminis	*P. recondita*	*P. striiformis*	*E. graminis*
Ae. tauschii	11,5	7,9	7,6	27,2
Ae. crassa	0	0	0	9,1
Ae. ventricosa	0	0	46,2	91,7
Ae. cylindrica	0	11,5	0	55,6
Ae. juvenalis	0	0	0	66,7
Ae. searsii	0	66,6	33,3	0
Ae. longissima				
ssp. *longissima*	0	25,0	28,6	85,7
ssp. *sharonensis*	12,5	12,5	18,8	100,0
Ae. bicornis	0	0	0	50,0
Ae. speltoides	80,8	90,4	82,7	78,0
Ae. peregrina	0	60,0	33,3	88,9
Ae. kotschyi	0	20,0	20,0	100,0
Ae. mutica	0	0	33,3	100,0
Ae. markgrafii	60,0	80,0	80,0	80,0
Ae. comosa	0	50,0	100,0	0
Ae. uniaristata	25,0	0	75,0	0
Ae. umbellulata	0	75,0	28,6	66,7
Ae. geniculata	36,8	12,1	51,6	91,2
Ae. neglecta	13,6	0	81,8	95,5
Ae. lorentii	0	55,6	50,0	100,0
Ae. columnaris	0	57,1	22,2	85,7
Ae. triuncialis	0	25,5	35,2	88,2
genus *Aegilops* (total)	18,6	24,6	33,3	64,2

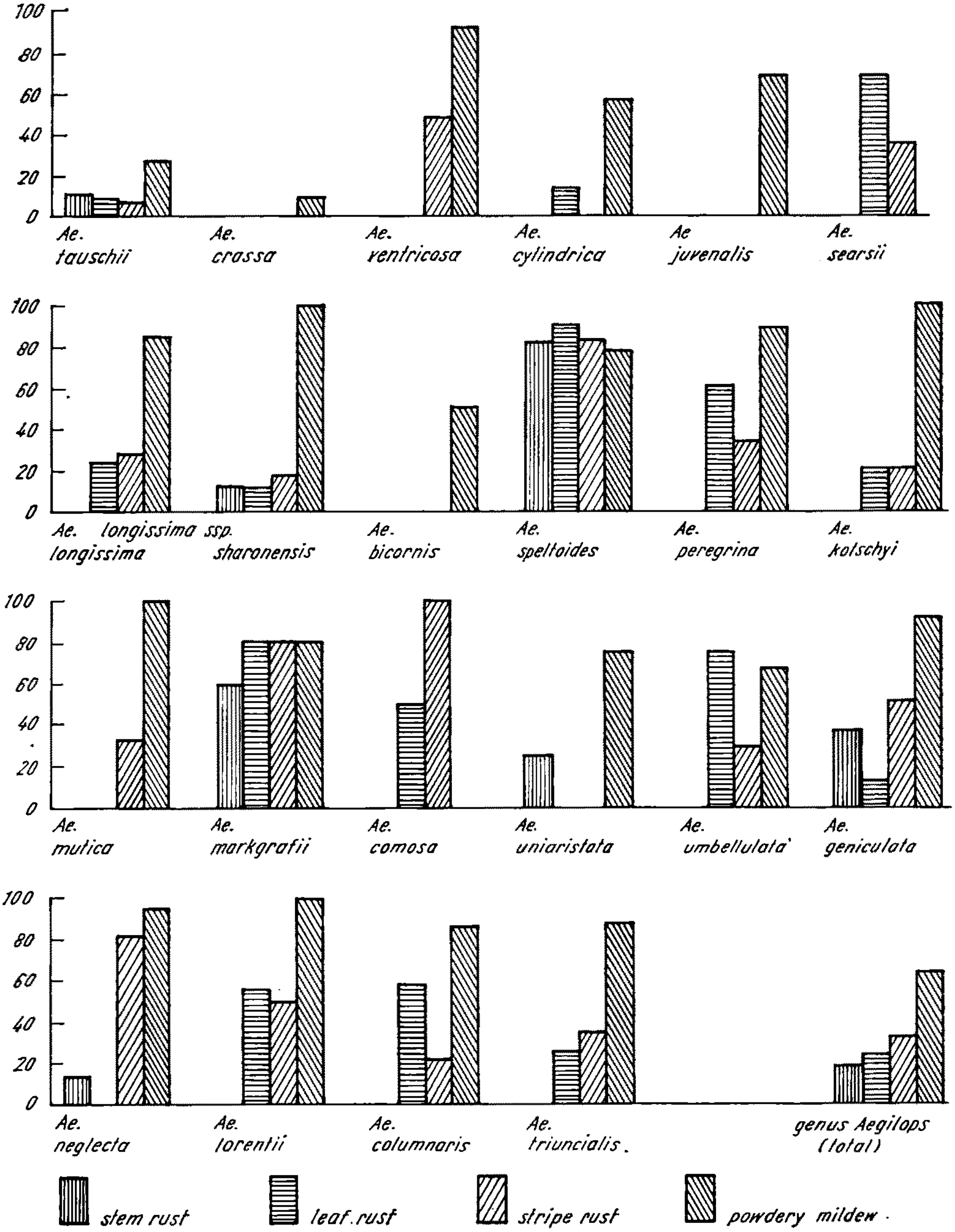

Fig. 1 Percentages of the resistant accessions (category R)

3.6. *Sources of disease resistance in Aegilops spp.*

During the disease resistance studies (Parts 3.1 to 3.5) substantial differences both in the resistance level and pattern were revealed among *Aegilops* species and accessions. Thus, it is conceivable that more sources of resistance can be found in some species than in the others. In the present paper it is impossible to describe all the resistance sources. Therefore, such accessions were selected within each *Aegilops* species whose resistance patterns express the whole range of resistance of the given species as fully as possible. These genetic resources of mostly combined resistance to several diseases are listed in Table 11. For the D genome donor, *Ae. tauschii,* more resistance sources are recorded because this species is recommended for the maximum exploitation in distant hybridization with wheat, owing to the homology of all its chromosomes with those of the D genome of the common wheat, *Triticum aestivum.* In spite of the relative susceptibility of *Ae. tauschii* several donors of combined resistance against two and more diseases have been discovered within the species (see Table 11).

In the polyploid species sharing the D genome with hexaploid wheats only the

Table 11

Resistance patterns of the selected sources of resistance

Species	Accession No.	*P. graminis*	*P. recondita*	*P. striiformis*	*E. graminis*
with homologous genomes					
a) the D genome donor					
Ae. tauschii	146	S	R	S	–
	190	MR	R	R	R
	192	R	PR	PR	S
	202	R	PR	R	MR
	213	R	R	R	S
	248	R	R	S	S
	255	S	PR	R	R
	259	S	PR	R	S
	260	S	R	R	R
	426	S	S	R	S
b) sharing the D genome					
Ae. crassa	568	S	S	PR	R
Ae. ventricosa	484	S	PR	R	R
Ae. cylindrica	435	S	R	S	R
Ae. juvenalis	182	S	S	PR	R
with homoeologous genomes					
a) closely related					
Ae. searsii	640	S	R	R	–
Ae. longissima ssp. *longissima*	122	S	R	R	R
Ae. longissima ssp. *sharonensis*	409	R	R	R	R
	413	R	R	R	R
Ae. bicornis	106	S	S	PR	R
Ae. speltoides	324	R	R	R	R
	330	R	R	R	R
	405	R	R	R	R
	523	R	R	R	R
	554	R	R	R	R
Ae. peregrina	539	S	R	R	R
Ae. kotschyi	120	S	R	R	R

Table 11 (continued)

Species	Accession No.	*P. graminis*	*P. recondita*	*P. striiformis*	*E. graminis*
b) less closely related					
Ae. mutica	127	S	PR	PR	R
Ae. markgrafii	107	R	R	R	R
	574	R	R	R	R
Ae. comosa	116	S	R	R	S
Ae. uniaristata	576	R	PR	R	S
Ae. umbellulata	151	S	R	R	–
Ae. geniculata	68	R	R	R	R
	441	R	R	R	R
Ae. neglecta	584	R	PR	R	R
Ae. lorentii	391	S	R	R	R
Ae. columnaris	111	S	R	MR	R
Ae. triuncialis	364	S	R	MR	R
	370	S	PR	R	R

powdery mildew resistance is relatively frequent, but *Ae. ventricosa* (AE 484) could be also the donor of resistance to stripe rust and *Ae. cylindrica* (AE 435) to leaf rust.

Ae. speltoides is a unique species not only in the group of the closely related species but in the entire genus *Aegilops* considering its exceptional resistance to all four diseases. Therefore, only five representatives are presented in Table 11 but in this species the total number of sources with complete resistance is much higher.

Other two donors of complete resistance were surprisingly found in *Ae. longissima* ssp. *sharonensis*, otherwise a relatively susceptible subspecies. The resistance patterns of sources of combined resistance in *Ae. longissima* ssp. *longissima*, *Ae. peregrina* and *Ae. kotschyi* correspond to those of their respective species. Accession AE 640 of *Ae. searsii* should be considered with caution because its resistance was tested only with a single isolate of stripe rust.

In the less closely related species with homoeologous genomes the donors of complete disease resistance occur in *Ae. markgrafii* and *Ae. geniculata*. The representatives of *Ae. lorentii* and *Ae. neglecta* possess combined resistance to three diseases. Other selected genetic resources of the group are donors of combined resistance to two diseases with the exception of the *Ae. mutica* accession which is resistant only to powdery mildew.

4. Discussion

In the present disease resistance study of the genus *Aegilops* the high total resistance to all pathogens was confirmed in *Ae. speltoides*. This result corresponds to the previous findings of other authors (HASSEBRAUK 1932 – cit. BELL and LUPTON 1955, MCFADDEN and RIVERS 1950, BELL and LUPTON 1955, HIRATSUKA 1955, GERECHTER-AMITAI 1967 – cit. FELDMAN 1979, MIGUŠOVA and GRIGOR'EVA 1973, PANAJOTOV and TODOROV 1979, PASQUINI 1980, ZITELLI 1980). Hence, it is necessary to consider this species as a valuable genetic resource of wheat in respect to disease resistance. Most *Ae. speltoides* genotypes induce homoeologous chromosome pairing in crosses with wheat (DVOŘÁK 1972). This behaviour was successfully employed in the transfers of resistance from this species to *Triticum aestivum* (DVOŘÁK 1977, SEARS, unpubl. – cit. DVOŘÁK and KNOTT 1980, MCINTOSCH et al. 1982). Until now, three leaf rust resistance genes and one gene for stem rust resistance have already been transferred from *Ae. speltoides* but its stripe rust and powdery mildew resistances have not yet been exploited. Existence of additional genes for resistance to the stem and leaf rust can also be assumed. Therefore, this allogamous diploid species should be submitted to a thorough genetic analysis of disease resistance and utilized intensively in distant hybridization with wheat. The transfer technique used by DVOŘÁK (1977) seems to be relatively simple and effective.

Another species with the high level of complete resistance to diseases is *Ae. markgrafii*. This is in agreement with previous authors (HASSEBRAUK 1932 – cit. BELL and LUPTON 1955, BELL and LUPTON 1955, MIGUŠOVA and GRIGOR'EVA 1973, PANAJOTOV and TODOROV 1979, PASQUINI 1980). Resistance genes of this species have not yet been transferred to wheat but owing to its excellent resistance more attention should be paid to *Ae. markgrafii* in distant hybridization. The crossing with wheat genotypes deficient in the Ph gene on chromosome 5 B (aneuploids or mutants) could be the appropriate method of the transfer. ABU BAKAR and KIMBER (1982) described genotypes of *Ae. markgrafii* which promoted homoeologous pairing in distant hybrids. If the donors of resistance described in the present paper belong to this category then the resistance may possibly be transferred by direct crossing with normal euploid forms of *T. aestivum*.

The diploid donor of the wheat genome D, *Ae. tauschii*, is not characterized by high resistance as a whole species (cf. KRIVčenko et al. 1984) but some accessions possessing combined disease resistances have been detected. Infraspecific variability in disease resistance was also reported by HIRATSUKA (1959). Two leaf rust resistance genes (Lr 21, Lr 22) and a gene of resistance to stem rust (Sr 33) were transferred from this species to wheat by KERBER and DYCK (1969, 1978). Due to the good homologous pairing of *Ae. tauschii* chromosomes with those of the D genome of hexaploid wheat (KIHARA 1944) its resistant accessions represent valuable genetic resources of cultivated hexaploid wheats. The usual method of gene transfer is performed via the production of synthetic hexaploids from crosses of *Ae. tauschii* with tetraploid wheats. Another possibility was suggested by SEARS (1981) which is based on the formation of semisynthetic hexaploid derivates after crossing *T. aestivum* with *Ae. tauschii* and then with tetraploid wheats.

Two accessions with complete disease resistance were detected in *Ae. longissima* ssp. *sharonensis*. Resistance of this subspecies to individual diseases was found by MCFADDEN and RIVERS (1950), HIRATSUKA (1955), MIGUŠOVA and GRIGOR'EVA (1973). For methods of transfer of the resistance see Introduction, but before the decision about their use is made it should be cytologically determined to which pairing type these accessions of *Ae. longissima* ssp. *sharonensis* belong. The same is true for the donors of combined resistance in *Ae. longissima* ssp. *longissima*.

As concerns the other diploid species both the resistances of *Ae. umbellulata* to leaf rust (Lr 9, transferred by SEARS 1956) and *Ae. comosa* to stripe rust (Yr 8, transferred by RILEY et al. 1968) were confirmed.

Ae. uniaristata was characterized by good resistance to stem rust (all its accessions are resistant or moderately resistant) so that in agreement with Pasquini (1980) this species is recommended as a donor of stem rust resistance.

Donors of complete disease resistance were detected in the polyploid species, *Ae. geniculata*, which was found to be disease resistant by Vavilov (1964). The resistance was later on confirmed by various authors. Until now, no resistance genes have been transferred to wheat. Therefore, *Ae. geniculata* still remains to be an important potential genetic resource of resistance to diseases for wheat. The induction of homologous pairing in the absence of the Ph suppresor on 5 B chromosome or the production of translocations by irradiation of hybrids may be utilized in gene transfers to wheat.

In the other polyploid species of the subgenus *Aegilops* some accessions possess combined disease resistance which could be exploited by similar methods as mentioned above in *Ae. geniculata.*

Polyploids, containing the common genome D, are generally more susceptible but sources of combined resistance to two diseases occur in *Ae. cylindrica* and *Ae. ventricosa*. The homologous pairing of the D genome chromosomes with those of wheat should be preferentially used in the gene transfer but it must be taken into account that the resistance genes can be located on the nonhomologous genomes as it was found by Dosba et al. (1978).

In conclusion it has to be stressed that in some cases the transfer of the resistance may at present prove to be difficult or impossible because of the complicated genetic basis of the resistance and/or the existence of undesirable interactions of the resistance genes with the genetic background of wheat (partial or complete inhibition of resistance). Recent results indicate that the inhibition of disease resistance may by a more frequent phenomenon in wheat than it was supposed earlier (Kerber and Green 1980, Košner and Bartoš 1982, Kerber 1983).

The results of this study demonstrate a considerable variability of disease resistance within the genus *Aegilops* and also within a majority of species of the genus. A great number of potential donors of complete, combined or single resistance to cereal rusts and mildew was discovered. Therefore, the statement „das Gaterslebener *Aegilops*-Sortiment ist eine wichtige Quelle für Ausgangsmaterial zur Nutzung in Züchtungsforschung und Züchtung . . ." (Hammer 1980b) is fully justified.

Zusammenfassung

Krankheitsresistenz in der Gattung *Aegilops* L. – Schwarzrost, Braunrost, Gelbrost und Mehltau

Die Gaterslebener *Aegilops*-Kollektion wurde auf Resistenz gegen folgende Weizen-Krankheiten untersucht: Schwarzrost *(Puccinia graminis)*, Braunrost *(Puccinia recondita)*, Gelbrost *(Puccinia striiformis)* und Mehltau *(Erysiphe graminis)*. Zahlreiche Quellen für Resistenz gegenüber einzelnen Krankheiten, kombinierte Resistenz und auch vollständige Resistenz gegenüber allen Erregern konnten unter den 487 Sortimentsnummern aus 21 *Aegilops*-Arten gefunden werden. Potentielle

Donoren mit vollständiger Resistenz wurden bei den diploiden Sippen *Ae. speltoides*, *Ae. longissima* ssp. *sharonensis* und *Ae. markgrafii* sowie bei der tetraploiden *Ae. geniculata* nachgewiesen. Methoden zur Übertragung der Resistenzgene von den einzelnen *Aegilops*-Arten auf den Weizen, *Triticum aestivum*, werden diskutiert.

Краткое содержание

Резистентность в роде *Aegilops* L. — Виды ржавчины и мучнистая роса

Гатерслебенская коллекция *Aegilops* исследовалась на резистентность к следующим возбудителям болезней пшеницы: *Puccinia graminis*, *P. recondita*, *P. striiformis*, *Erysiphe graminis*. Многие источники устойчивости к отдельным болезням, комбинированная устойчивость, как и полная резистентность ко всем возбудителям были найдены среди 487 коллекционных номеров 21 вида *Aegilops*. Потенциальные доноры, обладающие полной резистентностью были найдены у диплоидных форм *Ae. speltoides*, *Ae. longissima* ssp. *sharonensis*, *Ae. markgrafii* и у тетраплоидных *Ae. geniculata*. Обсуждаются методы переноса генов резистентности от отдельных видов *Aegilops* на пшеницу *Triticum aestivum*.

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