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Inheritance of resistance to *Ustilago nuda* (Jens.) Rostr. in some spring barley cultivars

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Abstract. The inheritance of resistance to loose smut (*Ustilago nuda*) in seven cultivars of spring barley has been examined. The performed studies showed that, resistance to two different groups of *U. nuda* races in respect of their virulence is determined by a single allele pair in the cvs. Anoidium and Inerme 2-r and by two allele pairs in the cvs. CI 13 662, Dorsett, Jet and OAC 21. In the cv. Abyssinian, resistance to a group of races 2 is determined by a single allele pair, whereas that to a group of races 4 – by two allele pairs. In all studied cultivars (except Anoidium) the resistance dominates over sensitivity. Resistance to the both studied groups of *U. nuda* races is determined by similar genes in the cvs. Dorsett and CI 13 662, as well as in Dorsett and OAC21, and additionally to a group of races 4 in the cvs. Abyssinian and OAC 21. No similarity was found between resistance genes in the case of two allele pairs in the cvs. Jet, Abyssinian and CI 13 662 (group of races 4) as well as in Jet, Dorsett and OAC 21 (in both groups of races), and in the case of a single allele pair in the cvs. Inerme-2-rowed and Abyssinian (group races 2).

Key words: barley, inheritance, resistance, ustilago nuda.

The so-far results of the studies show that resistance to *U. nuda* is chiefly determined by dominant genes, of which Un_1 was identified in the cv. Valentine (ANDREWS 1956), Un_2 – in the cv. Trebi, Un_3 and Un_6, Un_{11} and Un_{12} – in the cv. Jet, Un_4 – in the cv. Dorsett, Un_5 – in the line X-173-10-5-6-1 (SKOROPAD, JOHNSON 1952, KONZAK 1953, METCALFE 1962, METCALFE, HELGASON 1962, METCALFE et al. 1970, KOZERA 1975), Un_8 – in the cv. Milton and Russian (METCALFE, JOHNSTON 1963, MOSEMAN, METCALFE 1969), as well as Un_9 and Un_{10} – in the cv. OAC 21 (KOZERA 1979a). Only few investigators are of the opinion that resistance to loose smut is dependent on recessive genes,

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for instance, on un_7 in the cv. Anoidium (ANDREWS 1956) or on other unidentified genetic factors, which occur in the cvs. Missouri, B 696 or Saru 16 (SHANDS 1964, WOLFE 1976).

It follows from the attached data that resistance to *U. nuda* in different barley cultivars may have different genetic bases and according to the "gene-to-gene" theory may be dependent on genetic factors occurring in host plant, on the one hand, and on genetic basis of virulence of the pathogen biotypes occurring in a given area, on the other (DAY 1976, EENIK 1976). It should be mentioned that the absence of disease symptoms may be caused not only by a cultivar resistance, but also by the lack of inoculum of a pathogen or adequate races infecting certain genotypes. It may also be influenced by environmental conditions unfavourable to infection.

An important problem in breeding disease-resistant varieties are a discovery of new resistance sources and a knowledge on whether newly identified resistance genes are similar or different in relation to the so-far known. This is particularly important on account of various biotypes of the pathogen occurring in a given area. Varieties sensitive to certain races of a given parasite should not be cultivated in the areas where these races do occur.

The present study was carried out to show whether the genes identified in Poland (KOZERA 1979b), which condition resistance to *Ustilago nuda* (Jens.) Rostr., i.e. to its two biotypes different in respect of virulence, are the same or different. The studies were conducted in a complete cycle used in resistance breeding (F_1 to F_3).

Material and methods

Studies on similarity and difference of genes determining resistance to *U. nuda* in various cultivars of spring barley were conducted on the basis of 35 simple crosses. Parental components were nine cultivars of spring barley.

The parental forms used in the crosses were chosen on account of a maximal percentage of plant infection obtained during previous long-term investigations (KOZERA 1962, 1975, 1979a). The chosen forms were seven resistant cultivars (Abyssinian, Anoidium, CI 13 662, Dorsett, Inerme 2-r, Jet, OAC 21) and two cultivars (Ebro and Nigrum 10 345) susceptible to a group of *U. nuda* races differing in virulence.

Resistant genotypes were crossed with two sensitive cultivars, Ebro and Nigrum 10 345 (14 cross combinations), and to each other (21 cross combinations) (Table 1). It gave information on similarity or difference of resistance genes for seven unsusceptible cultivars studied.

Table 1. Crosses between barley cultivars, resistant and susceptible to *U. nuda*

Crosses between resistant forms	Crosses of resistant and susceptible forms
OAC 21 × Jet	Abyssinian × Ebro
OAC 21 × Inerme 2-r	Abyssinian × Nigrum 10 345
OAC 21 × Anoidium	
OAC 21 × Abyssinian	Aoidium × Ebro
OAC 21 × CI 13 662	Anoidium × Nigrum 10 345
OAC 21 × Dorset	
	CI 13 662 × Ebro
Jet × Inerme 2-r	CI 13 662 × Nigrum 10 345
Jet × Anoidium	
Jet × Abyssinian	Dorsett × Ebro
Jet × CI 13 662	Dorsett × Nigrum 10 345
Jet × Dorsett	
	Inerme 2-r × Ebro
Inerme 2-r × Anoidium	Inerme 2-r × Nigrum 10 345
Inerme 2-r × Abyssinian	
Inerme 2-r × CI 13 662	Jet × Ebro
Inerme 2-r × Dorsett	Jet × Nigrum 10 345
Anoidium × Abyssinian	OAC 21 × Ebro
Anoidium × CI 13 662	OAC 21 × Nigrum 10 345
Anoidium × Dorsett	
Abyssinian × CI 13 662	
Abyssinian × Dorsett	
CI 13 662 × Dorsett	

Hybrids of F_1 and F_2 generations were infected with two different groups of physiological *U. nuda* races: race 2 – the least virulent and race 4 – the most virulent among the so-far identified biotypes of this pathogen in Poland (KOZERA 1962, 1979b). Due to an artificial infection of hybrids their susceptibility, according to the biology of *U. nuda* development, was estimated the next year after the infection, i.e. in F_2 and F_3 generations. Susceptibility of F_3 plants to the pathogen was estimated on the basis of a separate multiplication of each studied plant, which enabled us to evaluate their genotypes. Susceptibility of F_2 plants was estimated on eighty plants and that of F_3 – on thirty plants.

Simultaneously with that a control inoculation was performed on the parental forms, the susceptibility of which was known (KOZERA 1962, 1975, 1979b). The purpose of such procedure was to eliminate the influence of weather conditions during plant infection upon the percentage of infected plants and the estimation of a maximal sensitivity of the parental forms. This is a more reliable criterion than calculation of an average plant infection. Plant infection

was carried out by the previously developed method (KOZERA 1962). Empirical and theoretical segregation ratios were compared by χ^2-values at P=0.99.

Results and discussion

The calculated values of the χ^2-test (Table 2) were used to establish whether resistance to *U. nuda* in the studied barley genotypes has a dominant or recessive character and whether it is determined by 1 or 2 allele pairs.

Table 2. The number of significant and nonsignificant χ^2values in F_2 and F_3 generations of 35 barley crosses (P=0.99)

Cultivar	Group of races 2				Group of races 4				Proposed no. of allele pairs	
	F_2		F_3		F_2		F_3		group of races 2	group of races 4
	1 allele pair	2 allele pairs	1 allele pair	2 allele pairs	1 allele pair	2 allele pairs	1 allele pair	2 allele pairs		
Abyssinian	0	2	0	1	1	0	2	0	1	2
Anoidium	0	1	0	2	0	2	0	1	1	1
CI 13 662	1	0	2	0	2	0	2	0	2	2
Dorsett	1	1	1	0	0	0	2	1	2	2
Inerme 2-r	0	0	0	2	1	1	0	2	1	1
Jet	1	0	1	0	1	0	1	0	2	2
OAC 21	0	0	1	1	2	0	1	1	2	2

Numbers in table: underlined mean the number of significant χ^2-values, not underlined mean the number of nonsignificant χ^2-values. On that basis it was inferred whether resistance in particular barley genotypes is determined by 1 or 2 allele pairs

On the basis of the number of significant and nonsignificant χ^2-values calculated for F_2 and F_3 generations as well as on the basis of the infection percentage (Table 3) it may be found that resistance to these both groups of *U. nuda* races in most studied cultivars (except Anoidium) has a dominant character. It should be also underlined that this resistance is completely of immune type only in the cvs. Jet and Inerme 2-r inoculated with a group of races 2 and 4, and in the cv. Dorsett inoculated with a group of races 4. In the remaining cultivars the infection percentage ranged from 7.6% in the cv. CI 13 662 to 16.3% in the cv. OAC 21 for a group of races 2 and between 3.4-20.2% in the same forms for a group of races 4 (Table 3). Though these

Table 3. Predominance of the action of genes of resistance to *U. nuda* in different unsusceptible barley cultivars on the basis of plant infection percentage in F_2 and F_3 generations

Group of races 4 / Group of races 2	Abyssinian (20.4%) 2p. allele		Anoidium (0.0%) 1 p. allele		CI 13 662 (3.4%) 2 p. allele		Dorsett (0.0%) 2 p. allele		Inerme 2-r (0.0%) 1 p. allele		Jet (0.0%) 2 p. allele		OAC 21 (20.2%) 2 p. allele	
	F_2	F_3	F_2	F_3	F_2	F_3	F_2	F_3	F_2	F_3	F_2	F_3	F_2	F_3
Abyssinian (15.8%) 1 p. allele	–	–	38.0 predominance of Abyssinian genes	4.3	0.0 predominance of CI 13 662 genes	6.1	37.9 predominance of Abyssinian genes	32.7	0.0 x	43.5 x	6.9 predominance of Jet genes	1.1	0.0 r	14.6 r
Anoidium (0.0%) 1 p. allele	8.9 predominance of Abyssinian genes	1.1	–	–	20.0 predominance of CI 13 662 genes	4.0	23.8 predominance of Dorsett genes	0.3	0.0 predominance of Inerme 2-r genes	0.0	0.0 predominance of Jet genes	0.7	10.0 predominance of OAC 21 genes	2.4
CI 13 662 (7.6%) 2 p. allele	0.0 x	9.0 x	14.3 predominance of CI 13 662 genes	26.4	–	–	0.0 r	2.3 r	5.5 x	6.2 x	0.0 predominance of Jet genes	0.1	0.0 predominance of CI 13 662 genes	1.0
Dorsett (10.4%) 2 p. allele	18.7 x	14.4 x	11.8 predominance of Dorsett genes	13.8	27.3 r	1.7 r	–	–	0.0 x	0.0 x	0.0 predominance of Jet genes	0.0	0.0 r	24.6 r
Inerme 2-r (0.0%) 2 p. allele	0.0 predominance of Inerme 2-r genes	0.0	0.0 predominance of Inerme 2-r genes	0.0	0.0 x	0.0 x	0.0 x	0.0 x	–	–	0.0 x	0.0 x	0.0 x	0.0 x
Jet (0.0%) 2 p. allele	4.2 x	1.4 x	0.0 predominance of Jet genes	0.8	0.0 predominance of Jet genes	0.0	0.0 predominance of Jet genes	0.0	0.0 x	1.4 x	–	–	2.8 predominance of Jet genes	6.7
OAC 21 (16.3%) 2 p. allele	0.0 x	13.7 x	6.0 predominance of OAC 21 genes	8.3	0.0 predominance of CI 13 662 genes	4.7	0.0 r	14.3 r	0.0 x	7.7 x	0.0 predominance of Jet genes	12.6	–	–

N o t e: the maximum infestation by 2 or 4 *U. nuda* biotype is given in parantheses. x – a comparison of gene action is impossible because of a different allele number, r – equivalent genes.

forms show a certain damage after artificial infection, they can be referred to as resistant according to Roemer's scale (KOZERA 1962). Because of their full resistance in field conditions they were included in the research programme concerning the assessment of genes' similarity.

As mentioned above, taking into account the percentage of F_2 and F_3 plant infection, only in the cv. Anoidium the resistance to *U. nuda* seems to have a recessive character (in crosses involving Anoidium the predominance of

Table 4. Theoretical segregation ratios (in % of infected plants) in F_2 and F_3 hybrids originating from crossing barley genotypes of different resistance assuming that resistance is determined by 1 or 2 gene pairs

Crosses between parental forms of different genotypes	Theoretical segregation ratios	
	F_2	F_3
	resistant : susceptible	resistant : susceptible
2 pairs of dominant resistance genes × 2 pairs of dominant resistance genes	100 : 0	100 : 0
2 pairs of dominant resistance genes × 2 pairs of recessive susceptibility genes	94 : 6	86 : 14
1 pair of dominant resistance genes × 1 pair of dominant resistance genes	100 : 0	100 : 0
1 pair of dominant resistance genes × 1 pair of recessive susceptibility genes	75 : 25	62 : 38

the gene originating from this cultivar is missing). This observation is in agreement with the result of ANDREWS (1956), who designated a recessive gene in Anoidium as un_7. A dominant character of resistance to *U. nuda* in most cultivars, which was observed in the present work, is also supported by results of other investigators (KONZAK 1953, METCALFE, JOHNSTON 1963, METCALFE et al. 1970, KOZERA 1975, 1979a).

An analysis of preliminary results concerning infestation of F_2 and F_3 hybrids from crossing resistant and susceptible cultivars (Ebro and Nigrum 10 345), besides finding whether resistance is a dominant or recessive character in relation to the pathogen biotypes occurring in Poland, permitted to establish how many gene pairs determine this character. As seen from the data of Tables 2 and 4, resistance to the both groups of *U. nuda* races is determined by one allele pair in the cvs. Anoidium and Inerme 2-r, and by two allele pairs in the

forms CI 13 662, Dorsett, Jet and OAC 21. Only the cv. Abyssinian showed differentiation in the inheritance to *U. nuda* susceptibility in relation to the studied pathogen biotypes. Resistance in that form to the group of races 2 was determined by a single allele and that to the group of races 4 – by two allele pairs.

The monogenic character of resistance to *U. nuda* found in the present work was also observed by other authors in the cvs. Abyssinian (MOHAJIR et al. 1952) and Anoidium (ANDREWS 1956). MOHAJIR et al. (1952) also reported that resistance to *U. nuda* in the cv. Abyssinian is determined by two pairs of genes. Likewise, KOZERA (1975, 1979a) found two pairs of resistance genes Un_9Un_{10} in the cv. Jet and $Un_{11}Un_{12}$ – in the cv. OAC 21. The inheritance mode of resistance described in the literature differs from that of the form CI 13 662 and Dorsett presented in the discussed studies. It was found that resistance in the form CI 13 662 is determined by gene Un_8 (SHANDS 1964, MOSEMAN, METCALFE 1969) and that in Dorsett – by gene Un_4 (SKOROPAD, JOHNSON 1952, SHANDS 1964, METCALFE et al. 1970), whereas as found in the present studies this character is determined by two pairs of alleles inherited independently of each other.

It also follows from the data of Tables 2 and 3 that genes which determine resistance of the studied barley cultivars to *U. nuda* are identical in relation to the both pathogen biotypes, extremely different in virulence. An exception, as mentioned before, is the cv. Abyssinian, in which the mechanism of inheritance to a group of races 2 is based on a single allele pairs and that to a group of races 4 – on two allele pairs. The above conclusion is based on the level of infestation by a group of races 2 and 4 of F_2 and F_3 hybrids (Table 3), obtained after crossing resistant forms. The obtained results are not always in agreement with studies of other authors reporting that inheritance of resistance to differential *U. nuda* biotypes may, though should not have the same character (METCALFE, JOHNSTON 1963, MOSEMAN, METCALFE 1969, KOZERA 1975, 1979a, THOMAS, METCALFE 1984).

On finding that resistance to the both *U. nuda* biotypes, different in virulence, is inherited in this way in the studied barley cultivars (except Abyssinian), a question arises whether resistance genes occurring in particular cultivars are the same or different. It, therefore, is necessary to consider first of all similarity between the genes in cultivars, the resistance of which is determined by a single pair of alleles. In this case, as seen from the data of Tables 2 and 3, effects of resistance gene action are stronger in the form Inerme 2-r than in the cvs. Abyssinian (group of races 2) and Anoidium (group of races 2 and 4). When resistance is determined by two allele pairs, effects

of gene action in the cv. Jet are stronger than in the cvs. Abyssinian (group of races 4), CI 13 662, Dorsett and OAC 21 (in both races) (Tables 2, 3). Genes are stronger in their action in the cv. CI 13 662 than in the cv. Abyssinian (group of races 4) and OAC 21 (both races). It was found that effects of genes occurring in the cv. Dorsett are stronger only than those in the cv. Abyssinian (group of races 4) and are similar to those occurring in the cvs. CI 13 662 and OAC 21 (both races). Genes of the cvs. OAC 21 and Abyssinian (group of races 4) are similar in their action.

A monogenic inheritance of resistance to *U. nuda* in the cvs. Dorsett and CI 13 662 is different from the inheritance mechanism of these forms resistance to biotypes of *U. nuda* occurring in Poland. This difference, as mentioned before, is connected with the herein found genetic determination of these cultivars resistance by two, not one allele pairs as well as with the fact that resistance genes in these forms are probably identical (Table 3). It, therefore, may be suggested that gene Un_4 identified by other authors in the cv. Dorsett (SKOROPAD, JOHNSON 1952, SHANDS 1964, METCALFE et al. 1970) as well as gene Un_8 in the cv. CI 13 662 (SHANDS 1964, MOSEMAN, METCALFE 1969) are not identical to presently defined genetic factors.

The only cultivar, the resistance of which is probably determined by recessive genes, is Anoidium. It was reflected in the results presented in Table 3 which indicate that the action of resistance genes in all unsusceptible studied forms of barley in comparison with Anoidium is stronger and independent on the inheritance mode (one or two allele pairs). It, therefore, may be assumed that recessive gene un_7 (ANDREWS 1956) identified previously in the cv. Anoidium is probably identical to a gene determining resistance of that cultivar to the pathogen biotypes occurring in Poland.

Summing up the obtained results it may be inferred that in all studied forms (except Anoidium) the resistance is dominant. In the cvs. Anoidium and Inerme 2-r, resistance to the both studied groups of *U. nuda* races is determined by one allele pair, whereas that in the cvs. CI 13 662, Dorsett, Jet and OAC 21 – by two allele pairs. Resistance of the cv. Abyssinian to a group of races 2 is determined by a single allele pair and that to a group of races 4 – by two allele pairs. In the case of artificial infection, resistance genes determine immune resistance to both groups of *U. nuda* races in the cvs. Inerme 2-r and Jet and besides, to a group of races 4 in the cv. Dorsett. In the remaining cultivars (CI 13 662, OAC 21) they determine resistance within 10-16% in the case of the group of races 2 and from 3% to 20% of plant infestation in the case of the group of races 4. Similarity of resistance genes to the both studied groups of *U. nuda* races was revealed in the cvs. Dorsett and CI 13 662 as

well as Dorsett and OAC 21, and besides that, resistance to a group of races 4 was found in the cvs. Abyssinian and OAC 21.

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