

Is the cereal rust mite, *Abacarus hystrix* really a generalist? – Testing colonization performance on novel hosts

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Abstract. The majority of eriophyoid mites are highly host specific and restricted to a narrow range of acceptable host plant species. The cereal rust mite, *Abacarus hystrix* was considered to be one of a few exceptions among them and has been found to be using a relatively wide host range. Since this species is a vagrant, inhabiting short-lived plants and aerially dispersing, it has commonly been considered to be a host generalist. Here the opposite hypothesis is tested, that host populations of *A. hystrix* are specialized on their local host plants and may represent host races. For this purpose, females from two host populations (quack grass, *Agropyron repens* and ryegrass, *Lolium perenne*) were transferred, and subsequently reared, on their normal (grass species from which females came from) and novel (other grass species) hosts. The female's fitness was assessed by survival and fecundity on the normal and novel host. Females of both populations had no success in the colonization of the novel host. They survived significantly better and had significantly higher fecundity on their normal host than on the novel one. These findings correspond with observations on host-dependent phenotype variability and host acceptance. The presence of locally specialized host populations in *A. hystrix* may be evidence for high host specificity among eriophyoids and the viruses they transmit. The main conclusion is that *A. hystrix*, which so far has been considered as a host generalist, in fact may be a complex species consisting of highly specialized host races.

Introduction

Eriophyoid mites are obligately adapted to live and feed on plants (Lindquist and Oldfield 1996). They are host specific and mostly restricted to a narrow range of acceptable host plant species. The majority of eriophyoid species have been reported from a single host species or species within a single genus (Oldfield 1996; Sabelis and Bruin 1996). The host generalist strategy is considerably less common among eriophyoids. Among at least 3761 described species, only several are known using a relatively wide host range, e.g. *Aceria malherbae* Nuzzaci, *A. tenuis* (Nalepa), *A. tulipae* (Keifer), *Aculus schlechtendali* (Nalepa), *Calacarus citrifolii* Keifer (Smith Meyer 1981; Oldfield 1996; De Lillo and Amrine in preparation).

Most information on relationships between eriophyoid mites and their hosts has been inferred from observations on prevalence, intensity of infestation or degree of plant damage on certain hosts (e.g. Herbert 1974; Vaneckova-Skuhrava 1996; Coyle and Amrine 2004; Skoracka 2004). Such studies, however, resulted in the reporting of eriophyoid host ranges only, but not in describing the mechanisms determining host ranges. The host specificity and plant–mite relationships cannot be explained without testing the host suitability and susceptibility to mites (by measuring mite preference, acceptance or performance). Such observations are numerous for tetranychid mites (e.g. Fry 1989, 1999; Gotoh et al. 1993; Yano et al. 1998; Agrawal 2000; Egas and Sabelis 2001), and comparatively scarce for eriophyoid mites. This may be due to the rearing problems and to the relatively low economic relevance compared to tetranychid mites. From our knowledge, there are only a few works focusing on the colonization of different hosts by eriophyoid mites (Bergh and Weiss 1993; Hong et al. 1998; Harvey et al. 2001). More studies concentrated on the host specificity of species which may be used for biological control of weeds, i.e. *Aceria tamaricis* (Trotter) (De Lillo and Sobhian 1994), *A. chondrillae* (G. Can.) (Caresche and Wapshere 1974; Cullen and Moore 1983), *Aceria centaureae* (Nalepa) (Sobhian et al. 1989), *A. salsolae* De Lillo et Sobhian (Sobhian et al. 1999), *Cecidophyes rouhollahi* Craemer (Sobhian et al. 2004), *Epitrimerus taraxaci* Liro (Petanovic 1990), *Phyllocoptes nevadensis* Roivainen (Littlefield and Sobhian 2000), *Floracarus perrepae* Khinicki et Boczek (Freeman et al. 2005). Despite the above examples, knowledge of host specificity in eriophyoids is still insufficient.

The cereal rust mite, *Abacarus hystrix* (Nalepa) is one of a few exceptional species among eriophyoids that has been found on a great variety of plants. It has a world-wide distribution and up to now at least 75 grass species have been recorded as its hosts (De Lillo and Amrine in preparation). Many of these grasses represent a significant component of the cultivated ecosystems, in which *A. hystrix* causes economic losses (Frost and Ridland 1996). Having a wide host range, this species seems to be an adequate object for studying mite specificity and mechanisms determining mite–host relationships. Moreover, earlier studies showed that specific hosts may have an effect on the population growth and also on the mite phenotype. The former effect has been documented by Gibson (1974) through observations on the feeding behaviour of this mite on a number of grass species. Also, a survey carried out in Poland has revealed that among 37 grass species, on which *A. hystrix* was found, only 12 were identified as specific hosts, 17 others as accessory and eight as accidental hosts (Skoracka 2004).

The effect of the host plant on phenotype of the cereal rust mite has been previously shown by morphological examination of populations of *A. hystrix* collected from three different hosts (Skoracka et al. 2002). As a result, an apparent host-related variation in quantitative morphological traits of the cereal rust mite has been found. Other observations showed that between host populations of *A. hystrix* there are considerable differences in host acceptance

manifested behaviourally (Skoracka and Kuczyński 2005). These findings dispose us to hypothesize that host populations of *A. hystrix* represent host races. The aim of the present study is to test the above hypothesis by comparing the fitness of females, assessed by survival and fecundity, between the normal and a novel host plant.

Materials and methods

We have chosen two populations of the cereal rust mite, one from quack grass *Agropyron repens* (hereafter A-population), and one from ryegrass *Lolium perenne* (hereafter L-population). Both grass species are of economical relevance. *Lolium perenne* is a cultivated species, *A. repens* is a weed. Both species are known to be infected with plant viruses (AMV and RMV) transmitted by *A. hystrix* (Oldfield and Proeseler 1996).

Grass cultivations and stock mite colonies

Quack grass rhizomes and ryegrass seeds were obtained in October 2003 from two separate study plots in Poznań, Poland (ryegrass: E16°52.5', N52°26.5' and quack grass: E16°53.0', N52°24.5'). Plant propagative parts were put in boxes with sandy and brown soil, respectively. Grasses were kept at room temperature and exposed to artificial light during 19 h per day. To protect plant from infestation by mites, insects or fungi boxes were covered with nylon taffeta fastened to the wooden frame. When grown-up, plants were used for the preparation of stock mite colonies and experiments.

Stock colonies of mites were established with individuals collected on quack grass and ryegrass from the same study plots as grass species during November 2003. Females from grass of a given species were randomly selected and transferred to uninfested plants of the same species. A detailed description of the stock colony preparation can be found elsewhere (Skoracka and Kuczyński 2004). Both colonies were maintained separately in two controlled-environmental chambers (20 °C, 85% ± 1 RH; 17–18/6–7 L:D) for 8 weeks. Afterwards, the mites were used for the trials.

Experimental design

The procedure of preparing plants for trials is described in Skoracka and Kuczyński (2004).

Two components of fitness were measured: fecundity (by estimation of the mean number of eggs) and survival (the percentage of survived females). Both fecundity and survival were estimated for A-population and L-population separately, when reared on the same grass species as in a stock colony (normal

host) and on the opposite grass species (novel host). For this purpose females or female nymphs of each of two examined populations were transferred from the stock colony to a normal or novel host plant. All possible combinations (hereafter trials) were tested: (1) AA – females from quack grass transferred to quack grass (normal host); (2) AL – females from quack grass transferred to ryegrass (novel host); (3) LL – females from ryegrass transferred to ryegrass (normal host); (4) LA – females from ryegrass transferred to quack grass (novel host). These abbreviations are used in the table and figures.

For all trials three tests were performed.

Test 1

Females of unknown age (probably fertilized) were transferred from the stock colonies to the normal host plants or to the novel host plants. Between 13 and 15 females were placed on one leaf. During, or immediately after the transfer, some females fell down. Such specimens were not included in further observations. After a few hours (2–3) experimental leaves were checked and females were counted. Thus, the number of specimens included in the test might be different from the number of females initially placed on the experimental leaf (however, it was never smaller than 10 specimens). The total number of specimens tested is given in Table 1. Plants were subsequently controlled every 8 h during 80 h, and then the trials were terminated. Only females were counted. Data obtained during this test allowed estimates to be made of the survival curves of fertilized females (of unknown age) within the 8-h interval.

Test 2

This test was prepared in a similar way as the test no. 1 with a few minor but important differences. Plants were controlled every 48 h during 10 days, numbers of females (alive and dead) and eggs were counted. After the 10th day the experimental trials were terminated. Data obtained during this test allowed estimates to be made of the survival and fecundity of fertilized females (however, of unknown age) within the 48-h interval.

Table 1. Summary of experimental procedures: number of experiment repetitions and sample size used for estimation of female survival and fecundity.

Trial	Test 1 (8-h interval)		Test 2 (48-h interval)		Test 3 (24-h interval)	
	No. of repetitions	<i>n</i>	No. of repetitions	<i>n</i>	No. of repetitions	Duration (days) <i>n</i>
AA	6	65	14	184	10	11–30 24
AL	6	100	19	274	9	1–11 23
LL	7	105	16	201	11	11–22 20
LA	5	73	14	198	8	5–11 24

Legend: *n* = the total number of females (for tests 1 and 2) or female nymphs tested (for test 3).

Test 3

Female quiescent nymphs were transferred from the stock colonies to the normal or novel host plants. Between 1 and 5 nymphs were placed on one leaf. This number was constrained by the number of nymphs ‘available’ in the stock colony. Nymphs were regarded as ‘available’ if they were guarded by at least two males, which indicated that the nymph is a female. Males of *A. hystrix* guard female nymphs soon before their emergence (personal observation). When at least one nymph was ‘available’ we used it for the experiment. Plants were controlled every 24 h, numbers of females (both alive and dead) and eggs were counted. The experimental trials were terminated when all females died or left the plant or when the leaf of the plant faded due to mites feeding. Data obtained during this test allowed estimates to be made of the survival and fecundity of unfertilized females within the 24-h interval.

All experiments were conducted in controlled-environment chambers (20 °C, 85% ± 1% RH; 17–18/6–7 L:D), each trial separately. Table 1 summarizes the trials and tests performed.

Data analysis

Survival curves were fitted with the Kaplan–Meier method for each of the trials within three tests separately. Data set-up of the form (t_i, u_i) was used, where t_i is the observed survival time of an adult mite and $u_i = 0$ if the observation was censored (i.e., the mite was not further observed and its fate was unknown) or $u_i = 1$ if death was stated (Hosmer and Lemeshow 1999). Survival curves were compared using the test of Harrington and Fleming (1982).

The age-dependent fecundity was not possible to estimate since the age of fertilized females was unknown. Thus, the fecundity was calculated as a mean number of eggs per female during its life. Fecundity was assessed for test no. 2 and 3 only, since the test no. 1 lasted 80 h and this period was too short for fecundity estimation. Means are given with 95% confidence intervals (CI hereafter), and were regarded as ‘significantly different’ when their CI did not overlap. CI were computed using the bootstrap method (Efron and Tibshirani 1993). For all computations the S-PLUS software was used.

Results

Survival

Both females of the A-population (from quack grass) and the L-population (from ryegrass) survived significantly better on their normal host (trials AA, LL) than on the novel host (trials AL, LA) (H-F test between the survival curves $p \ll 0.0001$ in all cases). This pattern is repeatable within all three tests performed (Figure 1).

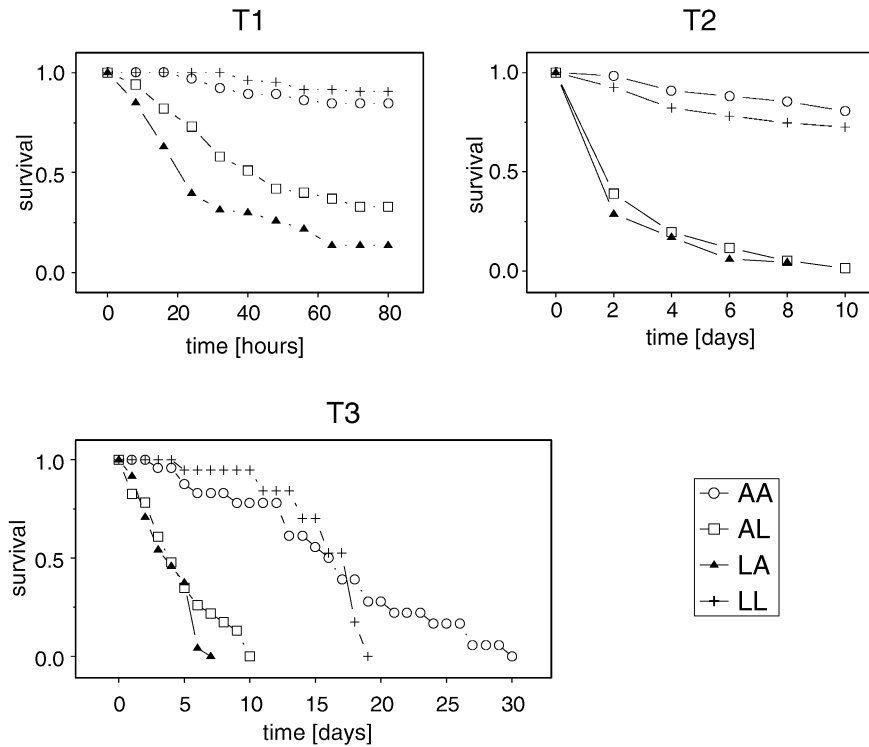


Figure 1. Survival curves of females of *Abacarus hystrix* reared on their normal (trials AA and LL) and novel hosts (trials AL and LA). Legend: T – test; T1: fertilized females, 8-h interval, T2: fertilized females, 48-h interval, T3: unfertilized females, 24-h interval.

The mean longevity of females of both populations was longer when they were reared on their normal (trials AA, LL) hosts comparing to novel hosts (trials AL, LA) within all three tests performed (Figure 2).

Fecundity

Females of both populations had significantly higher fecundity on their normal hosts (trials AA, LL) when compared to novel hosts (trials AL, LA) (Figure 3). Even if some eggs were deposited on the novel hosts no adults of F1 were noticed. This is true for both unfertilized and fertilized females.

Discussion

The results support the hypothesis of the existence of specialized host races in *Abacarus hystrix*. Mites both from quack grass and ryegrass have no success in

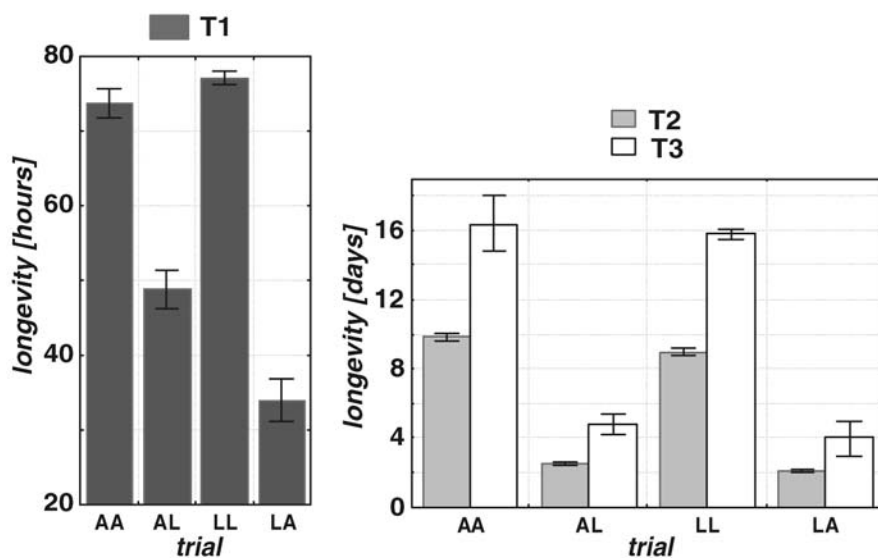


Figure 2. Mean (\pm SE) longevity of females of *Abacarus hystrix* reared on their normal (trials AA, LL) and novel hosts (trials AL, LA). Legend: T – test; T1: fertilized females, 8-h interval, T2: fertilized females, 48-h interval, T3: unfertilized females, 24-h interval.

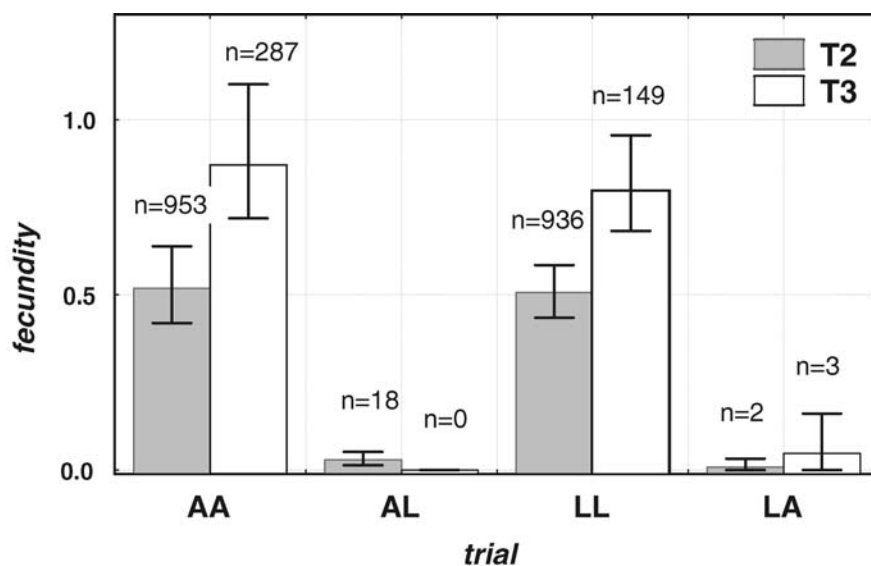


Figure 3. Fecundity (eggs/female/day) of females reared on their normal and novel hosts. Legend: T – test; T2: fertilized females, 48-h interval, T3: unfertilized females, 24-h interval; n = the total number of eggs oviposited throughout the trial. Bars represent 95% CI around means.

the colonization of the novel host plants. The females of both populations survived better on their normal host than on the novel one. The fecundity on the novel host was extremely low or zero. These results were consistent within all experiment repetitions as well as the three variants tested.

The existence of 'biotypes' of the cereal rust mite adapted to specific members of the Poaceae has been already suggested by Gibson (1974). He showed that *A. hystrix* from ryegrass is able to colonize only *Lolium* spp. and *Festuca pratensis*, and not able to develop on timothy, maize, barley, oats and wheat. Our earlier observations are also in agreement with present results. Studying morphological variation of *A. hystrix* we found significant differences in the body shape and overall body size among ryegrass and quack grass populations (Skoracka et al. 2002). Other studies showed that the same host populations of *A. hystrix* differ significantly in their life-history traits, such as developmental time, female survival and ovipositional strategies (Skoracka and Kuczyński submitted). Such differences in phenotype between populations using different resources suggest that populations may be host races (Diehl and Bush 1984).

However, the main condition for two or more populations to be considered as host races is their sympatric occurrence (Jaenike 1981). Hosts of the studied populations of *A. hystrix* (ryegrass and quack grass) are not geographically isolated, and between hosts mites are dispersed passively by wind (Nault and Styer 1969). Thus, it can be assumed that individuals in breeding conditions in one of the studied population are within normal cruising range of those in another studied population, i.e. both populations coexist in sympatry. Other criteria diagnostic of host races are that populations should show host preferences (Maynard Smith 1966; Bush 1975; Johnson et al. 1996) and host preferences should be positively correlated with host-specific fitness (Kondrashov and Mina 1986; Johnson et al. 1996). Measuring of host preference in eriophyoid mites meets some problems. First, the experiment in which mites would have strict choice of the host is difficult to arrange for eriophyoid mites, because they are slow-walking and have no adaptations that facilitate active finding a proper host (Lindquist and Oldfield 1996; Sabelis and Bruin 1996). Second, in the case of organisms which are dispersed by wind, host acceptance or rejection can be a more relevant measure of host plant selection than host choice, as it was suggested by Byrne et al. (1982) and Agrawal et al. (2002) for spider mites. We measured host acceptability of the cereal rust mite ryegrass and quack grass populations by comparing behaviour of females settled on each other's host (Skoracka and Kuczyński 2005). We found behavioural evidence of no acceptance of the novel host, which is associated with the lack of fitness on the novel host presented in this paper.

Thus, the studied host populations of *A. hystrix* meet the following criteria established for host races: sympatric coexistence, the use of different resources, differentiation of phenotypes and correlation between host acceptance and fitness. However, host races formation requires also positive assortative mating between individuals adapted to the same host plant (Bush 1975; Kondrashov and Mina 1986; Johnson et al. 1996). Mate choice is frequently a correlated

character of host preference (Johnson et al. 1996). Whether host-associated mating exist and is coupled with host acceptance in *A. hystrix* still required investigation. It is also evident that if host-race formation has occurred, then gene flow among host-associated populations should be restricted and genetic differentiation between populations is likely (Jaenike 1981; Waring et al. 1990). Such genetic differentiation should be spatially replicable, i.e. genetic differentiation between host races in sympatry should be greater than in some distant populations on the same host (Feder et al. 1990; Dres and Mallet 2002). Since, both cereal rust mite populations studied showed significant phenotypic differences and mites from ryegrass manifested no acceptance and were not able to survive and multiply on quack grass and vice versa, at least partial genetic separation between quack grass and ryegrass populations can be suggested. Thorough genetic studies of the host populations of *A. hystrix* should be, however, undertaken.

The evolution of host specificity is considered to be related to the relative availability and predictability of hosts. When hosts are predictable and abundant, parasites should specialize, and when hosts are in low abundance and ephemeral, parasites should generalize (Jaenike 1990). Host availability depends also on parasite dispersal abilities and the success rate of dispersing parasites to find and establish on a new host (Ward et al. 1998). *Abacarus hystrix* inhabits short-lived plants and disperses by wind currents (Nault and Styer 1969; Frost 1997), and during aerial dispersal the probability of finding a specific host is low (Sabelis and Bruin 1996). That is why it is hypothesized that host plant specialization in *A. hystrix* is not likely to evolve and the mite would have got a better success as a generalist (Sabelis and Bruin 1996). The present outcome, however, indicates that at least two host populations of *A. hystrix* are specialized in their host plant use and that host race formation is possible here.

The host specialization has been suggested also for other eriophyoid species. Sabelis and Bruin (1996) have given examples of polyphagous eriophyoids that may represent species complexes consisting of host-specific races, rather than exhibit species-wide polyphagy, e.g. monocot-infesting *Aceria* species (Shevchenko et al. 1970) and subspecies of *Aculodes mckenziei* (Keif.) (Sukhareva 1981). Caresche and Wapshere (1974) have shown that *Aceria chondrillae* (G. Can.) is highly specific to *Chondrilla* spp. However, the species has strains specialized to their usual host species in their respective geographical areas. The formation of host races is better known for spider mites (e.g. Gould 1979; Fry 1999; Gotoh et al. 1993; Agrawal 2000; Egas et al. 2003) and phytophagous insects (e.g. Via 1999; Dres and Mallet 2002; Ikonen et al. 2003; Blair et al. 2005; Forister 2005). This process is thought to be linked to disruptive selection exerted by different hosts and host-dependent trade-offs (Maynard Smith 1966). Many factors have been proposed to be important in determining the host specialization in phytophagous arthropods, e.g. secondary chemistry or nutrient content of plant (Dethier 1954; Bernays and Graham 1988), plant morphology (Kennedy 1986) or phenology (e.g. Filchak et al. 1999; Horner et al. 1999, see also Fox and Morrow 1981), host plant

abundance (Futuyma 1983, see also Fox and Morrow 1981) and natural enemies (Price et al. 1980; Bernays 1989). The present study did not focus on the factors that may determine the variation in performance of *A. hystrix* females on the familiar and novel host. Nevertheless, since these grasses are available for the cereal rust mite both spatially and temporally (making host plant shift likely to occur) the host plant chemistry and morphology or predators seem to be the most important factors determining host specialization. This hypothesis, however, needs to be investigated.

The existence of ryegrass and quack grass host races should be considered when studying the role of *A. hystrix* in viruses transmission. The mite is known as a vector of two viruses: RgMV – ryegrass mosaic virus (which infests perennial ryegrass and other *Lolium* spp.) and AgGM – agropyron mosaic virus (which commonly infests quack grass) (Oldfield and Proeseler 1996). However, the evidence indicates a high degree of host specificity between eriophyoids and the pathogens they transmit; one vector transmits just one agent and each pathogen is transmitted by just one species of eriophyoid (Krantz and Lindquist 1979). Sabelis and Bruin (1996) regard that “eriophyoid mites first had to develop some degree of host specificity to realize a condition for subsequent coevolution of the mutualistic virus–mite association”. So far only two grass-infesting species, *A. hystrix* and *Aceria tulipae*, were considered as vectors transmitting more than one pathogen (Oldfield and Proeseler 1996). Present results show that the relationship between RgMV and AgMV and their eriophyoid vectors may be highly specific. Since, population from ryegrass, which transmits RgMV, is not able to colonize quack grass, possibly it is also not able to transmit AgMV and vice versa.

To conclude, we found evidence that *A. hystrix*, which has commonly been considered as a host generalist, in fact may be a complex species consisting of populations highly specialized among its host plants. It cannot be said with certainty that all different host populations of the cereal rust mite represent different host races. It can be stated, however, that host race formation, and therefore gene pool separation, is possible in this species.

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