Evolution and ecology of *Puccinia graminis*

Vývoj a ekologie rzi *Puccinia graminis*

D. B. O. Savile and Zdeněk Urban

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Puccinia graminis subsp. *graminicola*, the rust of festucoid grasses in natural Bohemian and Slovakian "forest steppe", seems to be genetically close to ancestral *P. graminis* as it evolved in Eurasian vegetation. The complex makeup of recent mesic European pasture and meadow communities, in which several widely adapted grasses may persist indefinitely in close association, allows regular transfer of inoculum between such grasses; and this genetic "swamping" has prevented complete speciation by any rust strain. Selection of allopolyploid *Triticum* and *Avena* for cultivation, near the start of agriculture, allowed growth in one host, and then hybridization, of rusts adapted to individual parental diploid grasses. Gene exchange widened the host range of these hybrid rusts; but they are also possibly polyploids, for the spore protoplasts of *P. graminis* subsp. *graminis* vars. have markedly greater volumes than those of subsp. *graminicola*.

[1]) *Biosystematics Research Institute, Central Experimental Farm, Ottawa KIA OC6, Canada.* [2]) *Department of Cryptogamic Botany, Natural Science Faculty of Charles University 128 01 Praha 2, Benátská 2, Czechoslovakia.*

INTRODUCTION

Puccinia graminis PERS., *P. coronata* CORDA, and *P. recondita* ROB. ex DESM. (sensu lato) are extremely complex rusts with much less definite specific limits than most grass rusts or rusts of other plants. It has long been suspected that human activity throughout the development of agriculture has contributed to this bewildering complexity. Taking *P. graminis* as a model, we attempt to clarify the evolution of this important rust, in the hope that we may allow a better understanding of genetically complex rusts in general.

INFLUENCE OF EARLY AGRICULTURE

SAVILE (1971, 1979a) noted the genetic complexity of some important grass rusts, including *Puccinia graminis* PERS., and suggested that both ecological disturbance and selection of allopolyploids for cereals at the start of agriculture must have contributed to this complexity. Bringing together ecologically or geographically isolated grasses, whose diverging rusts had not yet reached genetic isolation, presumably produced some rusts with more complex genotypes and expanded host ranges. The early selection of allopolyploid cereals, culminating in hexaploid *Triticum aestivum* L. and *Avena sativa* L., in which the genomes of parental diploid ancestors were combined, presented the possibility that rusts compatible with two or even three

parental diploids might jointly attack the polyploids, which were no longer rare but were being abundantly propagated by man.

Mixed infection of the new allopolyploids would inevitably have resulted in hyphal fusions, nuclear exchanges and large-scale genetic recombination, as demonstrated in *Puccinia cruciferarum* RUD. (SAVILE 1964). Not only would such recombinants become further diversified in the dicaryotization process on the aecial host; but it is probable that parasexual recombination in repeating uredinial populations must occur. Although parasexuality is difficult to demonstrate experimentally in rusts, because of perpetual risk of contamination, it is the only reasonable explanation of a very distinctive high arctic rust, *Puccinia poae-nemoralis* OTTH subsp. *hyparctica* SAVILE, which must have diverged from parental *P. poae-nemoralis* after the onset of the Wisconsin glaciation. Although producing only urediniospores, and thus with no opportunity for normal meiosis, it differs markedly in the size, wall thickness, wall pigmentation, and pore number of the urediniospores, and in host specialization. If one does not suppose a pleiotropic mutational effect, each of these changes must have involved several mutations, and it is unrealistic to suppose that they all accumulated in a homogeneous population in about 50.000 years without substantial genetic recombination (SAVILE and PARMELEE 1964, SAVILE 1972).

SAVILE (1968, 1971, 1979a and b) emphasized the importance of jumps to ecogeographically associated and newly evolved plants as a means of speciation in rust fungi. This phenomenon was first documented in detail for the genesis of *Puccinia rufescens* on *Pedicularis* from *P. palmeri* on *Pentstemon* (SAVILE 1968). It is clear that jumps are integral to speciation in rusts, and many have been demonstrated (SAVILE 1979a) in various rust lineages on *Poaceae* and *Cyperaceae*, and in their derived autoecious rust groups.

INFLUENCE OF PREHISTORIC "FOREST STEPPE" AND RUDERAL GRASSLAND ECOLOGY

It now appears that SAVILE overlooked another complication. Dr. TAJIMI recently sent him copies of his excellent studies of the host ranges of five formae speciales of *Puccinia graminis*, from a journal not locally available (TAJIMI 1975, 1976, 1977, 1978, 1979). The data in these studies support an ecological effect opposite to that of jumps: that continuing strong ecological association between certain grasses is preventing speciation by some populations of *P. graminis* through a process of genetic "swamping".

TAJIMI used inoculum of five formae speciales of *Puccinia graminis* (*lolii, phlei-pratensis, dactylidis, tritici* and *poae*) to inoculate a wide range of festucoid grasses. Although formae speciales cannot be precisely defined, they are at least isolates that are compatible with the hosts from which they originated. TAJIMI recognized five degree of susceptibility in the inoculated hosts, of which the first two represent strong enough compatibility to indicate that the rust could persist indefinitely without additional inoculation; the next two are resistant reactions with a most small sori; and the last is essentially full resistance. His results show that most of the grasses that are compatible with two or more formae speciales are important and widely planted Eurasian forage grasses.

Table 1. Grasses widely compatible to *Puccinia graminis* in tests by TAJIMI

Tribe/Species	Rusts accepted[1]	Native range	Current status
Agrostideae			
Agrostis flaccida HACK.	(2), (5)	Japan	Mainly Japan
Alopecurus pratensis L.	1, (2), 5	Europe	Widespread
Phleum pratense L.	(1), (2)	Europe	Widespread
Aveneae			
Arrhenatherum elatius (L.)			
BEAUV. ex J. & C. PRESL	1, (3), 5	Europe	Widespread warm temp.
Deschampsia flexuosa (L.) TRIN.	1, (2), 5	Circumboreal	Minor forage value
Festuceae			
Dactylis glomerata L.	1, 2, 3, 5	Europe	Widespread
Festuca pratensis HUDSON	1, 2, 3, (5)	Europe	Widespread
F. rubra L. var. *rubra*	(2), (3)	Europe	Widespread
F. tenuifolia SIBTH.	1, (2), (5)	Europe	Mod. widespread
Lolium perenne L.	1, (2), (3)	Europe	Widespread
Poa pratensis L.	(3), 5	Europe	Widespread
P. sphondylodes TRIN.	(2), 5	E. Asia	Not Eur. or N. Am.
Phalarideae			
Phalaris arundinacea L.	1, 2, 5	Circumboreal	Also introd. N. Am.
Triticeae			
Elymus junceus FISCH.	(2), (3), (4)	E. Asia	Not Eur. or N. Am.
Hordeum glaucum STEUD.	(1), (2), (3), (4)	Mediterranean	Spreading as weed

[1] Numbers represent formae speciales used by TAJIMI: 1 = *lolii*, 2 = *phlei-pratensis*, 3 = *dactylidis*, 4 = *tritici*, 5 = *poae*. Open numbers represent full compatibility; and numbers in parentheses moderate susceptibility.

Because of the clear evolutionary implications of TAJIMI's findings SA-VILE presented the problem to URBAN, who has made ecological studies on rusts in bushy pastures with *Berberis vulgaris* of Czechoslovakia where sometimes various major forage grasses occur in habitats with secondary plant communities evolved under the influence of man.

Table 1 lists the grasses shown by TAJIMI to be fully or moderately compatible with two or more formae speciales of *Puccinia graminis*. *Agrostis flaccida*, *Poa sphondylodes* and *Elymus junceus* are species of eastern Asia that have not been significantly introduced as forage grasses in Europe or North America. *Hordeum glaucum* is a Mediterranean species that has spread as a weed in other parts of the world. *Deschampsia flexuosa* and *Phalaris arundinacea* are circumboreal; the former is of ecological rather than agricultural importance, but European strains of the latter have also been freely introduced into North America for forage use. The remaining nine species are of Old World origin but have been widely introduced from Europe into North America and elsewhere. *Festuca rubra* var. *rubra* is widely used as a lawn grass as well as for pastures. The others are all important forage grasses. Part of the value of these grasses lies in their wide ecological tolerances. They escape freely in eastern North America and persist indefinitely. In abandoned fields or other waste ground in Ontario it is commonplace to see several of them persisting in close association. Despite some differences in climatic tolerance, or occasionally soil preferences, it is notable that the detailed distribution maps of DORE and McNEILL (1980) for Ontario are remarkably similar for *Alopecurus pratensis*, *Phleum pratense*, *Deschampsia*

flexuosa, Dactylis glomerata, Festuca pratensis, F. rubra var. *rubra,* and *Poa pratensis. Arrhenatherum elatius* and *Lolium perenne* are climatically restricted to southern Ontario, but otherwise their patterns are similar. (The recurrent epithet *pratensis* emphasizes the place of some of these grasses in Europe).

To understand the importance of co-evolution of *Puccinia graminis* on grasses and its alternate host *Berberis* spp. we must consider the history of Central European (and Mediterranean) vegetation together with man's interference and changing influence. FRENZEL (1964) proposed that during the last (Würm) glaciation extensive grasslands, rich in various grass genera, must have existed east and north of the Alps in the lowlands of eastern Austria, Moravia and Bohemia, respectively. As forests readvanced in the Holocene the grasslands were reduced to islands in climatically and pedologically suitable localities. In the Neolithic, some 6—7000 years ago, man began destroy the integrity of the forests. Pasturing, especially, is responsible for damage to forests and changes in their flora. The original forest and forest-steppe vegetation belonging, in the lowlands and hilly regions, in the alliance *Carpinion betuli* (MAYER 1937) OBERDORFER 1953 or *Quercion pubescenti-petraeae* BR.-BL. 1931 began to be exploited so that besides the remnant original undergrowth and steppe flowers, there emerged newcomers (various forage grasses included) which gradually occupied pasture and meadow ecotopes owing to changing environmental factors conditioned by man. So it is very probable that in the times of Neolithic agriculture there existed in Bohemia and Slovakia a stem rust primarily of a "forest-steppe" origin — an ecosystem in which both graminicolous hosts and *Berberis* grow together.

The origin and evolution of pastures and meadows was here characterized by forest degradation subsequently followed by continuing invasion of forage grasses. The frequent association of two to several of these grasses with remnant grass species in prehistoric pastures and meadows evidently allowed enough gene-flow between partly host-specialized rust biotypes to prevent their complete speciation.

Simultaneously, the acreage of cultivated crop (wheat, barley etc.) mono-cultures became greater. In this way, a suitable precondition was formed for urediniospore long-distance spread of other rust populations adapted to non-alternation in vast steppe ecosystems more or less distant from barberies (URBAN 1968, 1969).

Thus the complexity of *Puccinia graminis* must be ascribed as much to the relatively unchanged and undisturbed evolution of the original rust as a component of the forest and "forest-steppe" ecosystem, as to the evolution of the same rust in steppes and artificial (man-made) uniform agroeco-systems whose range had been progressively increasing. URBAN (1980) has recently further emphasized the importance of the study of natural plant associations to the understanding of *Puccinia graminis* and some other rusts.

PROTOPLAST VOLUMES IN *PUCCINIA GRAMINIS* POPULATIONS

◤ In his taxonomic treatment of *Puccinia graminis*, URBAN (1967) recognized three morphologically distinct entities. *P. graminis* PERS. subsp. *graminis* was divided into two varieties: var. *graminis*, which includes the rust of *Triticum* but occurs on many other grasses; and var. *stakmanii* GUYOT,

MASSEN. et SACCAS ex URBAN, the rust of *Avena*, which also can attack various wild grasses. *Puccinia graminis* subsp. *graminicola* URBAN is typified by the rust of *Dactylis glomerata* in Bohemia, but it occurs freely on other festucoid grasses in various Bohemian plant associations (and, of course, is now practically world-wide). *Berberis vulgaris* is a natural element of some of these phytocoenoses and then its occurrence is correlated with that of *P. graminis* on adjacent grasses. *P. graminis* subsp. *graminicola* is evidently the natural rust of native festucoids in natural "forest-steppe" communities, and is probably little different from the ancestral form of *P. graminis*. A further indication that subsp. *graminicola* is the most primitive member of the complex is given by the urediniospore shapes. The broadly ellipsoid to ovoid spores of subsp. *graminicola* are typical of many rusts with equatorial urediniospore pores on both festucoid and especially various non-festucoid grasses. The long-ellipsoid to subcylindric spores of subsp. *graminis* var. *graminis* are exceptional among grass rusts, although linked to those of subsp. *graminicola* by subsp. *graminis* var. *stakmanii*. Although *P. graminis* subsp. *graminicola* attacks various native grasses it cannot attack cereals; but the cereal rust can attack some of these grasses as well as their normal hosts. It thus appears that the cereal rusts have more complex genomes than that of *P. graminis* subsp. *graminicola*.

These differences in scope draw attention to the differences in size of urediniospores and teliospores, by which these rusts are mainly distinguished. *Puccinia graminis* subsp. *graminicola* has the smallest spores; *P. graminis* subsp. *graminis* var. *stakmanii* has considerably larger spores; and those of *P. graminis* subsp. *graminis* var. *graminis* are even larger. Because of their complex and more variable shapes it would be difficult to estimate the cell volumes of the teliospores. However, urediniospores of a given subspecies or variety are more constant in shape, and are usually close enough to an ellipsoid in shape to allow a reasonably close estimate of the mean volume of the spore protoplasts, with the aid of models.

Using the figures of URBAN (1967) for mean urediniospore lengths and widths, the length: width ratio of each rust was obtained, which defines the shape of the ellipsoid. URBAN has recently calculated length : width. ratios for several more *P. graminis* populations, which show considerable variation. However, the same trend is evident; the urediniospores from cereals and *Agropyron repens* have high ratios, and those from most wildgrasses are low. The spore wall thicknesses average ca. 2,0 μm in the ends and 1,5 μm at the equator. Thus 4 μm is subtracted from the mean spore lengths and 3 μm from the widths to obtain the mean sizes of the protoplasts. To aid in estimating the volumes of the spore protoplasts a 30 mm diameter sphere was formed from modelling clay. Such a sphere has a volume of 14.130 mm³. From this sphere ellipsoids were formed to the shape of the mean spore protoplasts. Knowing that each of the clay ellipsoids had the volume of a 30 mm sphere, the mean length and width of the protoplast of each rust (in μm) had simply to be expressed as a ratio of those of the model (in mm) to give the equivalent sphere. The approximate volume of the equi .alent spheres was calculated from the familiar equation $V = 4/3\pi r^3$. The pertinent figures are recorded in Table 2. The appreciable variations n spore shape make exact volumes difficult, if not impossible to calculate.

; We see from Table 2 that the spore protoplast volume in subsp. *graminis* var. *stakmanii* is roughly 1.5 that in subsp. *graminicola*, and in subsp. *graminis* var. *graminis* it is roughly 1.8 times as big. Coupled with URBAN's indications that these two cereal rusts have wider host ranges than has subsp. *graminicola* (the native grass rust), these protoplast sizes suggest that the host ranges of the cereal rusts may involve more than simple gene exchange. It is conceivable that they are polyploids. Following authors: MCGINNIS (1953),

Table 2. Approximate mean urediniospore protoplast sizes, proportions and volumes for populations of *Puccinia graminis*

P. graminis PERS. population	L(ength) (μm)	W(idth) (μm)	Ratio L : W	Volume (μm³)	Volume : volume of *P. g. graminicola*
subsp. *graminis* var. *graminis* (*Triticum*)	28	14.6	1.918 : 1	2991	1.69
subsp. *graminis* var. *graminis* (*Triticeae*, gen.)	27.5	15.5	1.774 : 1	3295	1.87
Mean of above populations	27.75	15.0	1.85 : 1	3143	1.78
subsp. *graminis* var. *stakmanii* GUYOT et al. (*Avena*)	23	14.5	1.586 : 1	2571	1.46
subsp. *graminicola* URBAN (*Dactylis*, etc.)	19.5	13.5	1.444 : 1	1766	1.00

MACLEAN et al. (1971), WILLIAMS et al. (1971), VALKOUN et al. (1974) stated cerealicolous forms of *Puccinia graminis* and *P. recondita* as having chromosome number n = 6; in opposite McGINNIS (1954, 1956) found that *Puccinia coronata* from *Agropyron repens* and *Calamagrostis montanensis* in N. America possessed chromosome number n = 3. In flowering plant polyploidy is often, although not always, accompanied by increased cell size. See, e.g., BASSETT, MULLIGAN and FRANKTON (1962) and MOORE and LINDSAY (1953). The extremely small sizes of rust chromosomes make it so difficult to secure precise counts that a definite answer to this question may not be possible. Possibly the technique of cytofluorometry of DNA, described by WILLIAMS and MENDGEN (1975), will suggest an answer to the problem. If the rusts of *Triticum* and *Avena* do prove to be polyploid, their wide host ranges may be easier to understand,

ACKNOWLEDGEMENTS

SUMMARY

It appears that *Puccinia graminis* subsp. *graminicola* closely resembles the original *P. graminis* as it evolved in European, or Eurasian "forest steppe". In spite of partial specialization on individual grasses the complex constitution of such "forest steppe", with several widely adapted festucoid grasses often persisting indefinitely in close association, allowed regular transfers of rust biotypes between such grasses; and the resulting genetic "swamping" prevented complete speciation by any strain. The removal of ecological barriers with the spread of agriculture, and the repeated introduction of forage grasses, weedy grasses and cereals to new regions permitted additional gene exchange between previously isolated biotypes, which increased the complexity of the rust genomes. Selection of allopolyploid *Triticum* and *Avena* for mass planting as cereals made possible the intermingling of rust strains adapted to individual parental diploid plants, with altered genetic potential. Whether such changes occurred through simple genetic recombination or through the achievement of polyploidy remains undecided.

SOUHRN

Puccinia graminis subsp. *graminicola* parasituje na festukoidních travách v přirozených leso-stepních formacích Československa. Zdá se být vývojově blízká původní *P. graminis*, která se vyvíjela v některých euroasijských lesních a lesostepních formacích. Současné evropské mesické pastviny a louky s řadou široce přizpůsobitelných druhů trav umožňují, za přítomnosti dříšťálu, širokou vzájemnou výměnu inokula a genů; proto neprobíhá ostrá speciace a na různých lokalitách nalézáme různé speciální formy a rasy, které jsou si sadou hostitelů současně vzájemně podobné i rozdílné. Záměrný výběr alopolyploidů druhů rodů *Triticum, Avena* aj., který probíhá od dávných prvopočátků zemědělství, podmínil zprvu úzkou, avšak po hybridizaci daleko širší sadu hostitelů, v podstatě odrážející různé geny náchylnosti všech rodičovských diploidních druhů trav. Je možné, že při evoluci rzí a při vzniku jednotlivých taxonomických jednotek se uplatnila polyploidisace. Naznačovala by to skutečnost, že protoplasty urediniospor *Puccinia graminis* subsp. *graminis* mají zřetelně větší objem než protoplasty subsp. *graminicola*.

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R. Geesink, A. J. M. Leeuwenberg, C. E. Ridsdale, J. F. Veldkamp:

Thonner's analytical key to the families of flowering plants

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Recenzovaná kniha je celosvětový určovací klíč čeledí kvetoucích rostlin, který vznikl podstatnou úpravou, doplněním a přepracováním staršího díla vídeňského badatele Franze Thonnera čtyřmi výše jmenovanými holandskými autory. Tito autoři užívali Thonnerův klíč z r. 1917 při svých praktických cvičeních na univerzitě a shledali jej jako velmi vhodné dílo pro určování čeledí. Původní Thonnerův klíč měl 812 bodů — tezí a antitezí (vedle četných poznámek pod čarou), nynější upravený text má 2117 bodů. To ukazuje na podstatné přepracování původního textu, při němž byly respektovány také nové výsledky taxonomického a nomenklatorického studia na úrovni čeledi (zařazení nově popsaných čeledí, modernizace nomenklatury). Velká pozornost byla holandskými autory věnována tzv. aberantním rodům, jež často nelze určit společně s ostatními rody příslušné čeledi. Autoři se zároveň snažili použít takové znaky, jež je možno studovat převážně pouhým okem. Připojen je i návod k užití klíče a terminologický slovník.

Klíče čeledí se při určování naší flóry velmi často přecházejí, protože obvykle zařazení materiálu do čeledi je jasné a určování se počíná v čeledi nebo v rodu. Jiná je situace při určování herbářového materiálu z cicích území, živých rostlin v jiných květenných oblastech nebo rostlin pěstovaných, jež pocházejí z jiných regionů. Zde určení materiálu do čeledi má základní význam pro další určovací postup. Recenzent měl možnost využít tohoto klíče v několika obtížnějších případech a zjistil jeho plnou spolehlivost, zajištěnou pravděpodobně jeho dlouhodobějším užíváním na holandských univerzitách. Výhodou této příručky proti jiným obdobným klíčům je, že se vztahuje ke flóře celého světa.

Tato kniha nás také upozorňuje na zajímavou botanickou osobnost F. Thonnera, jenž měl i určité vztahy k naší vlasti. Jeho manželka Marie Svobodová byla Češka a sám Thonner strávil poslední léta svého života po první světové válce v Praze na Smíchově (v období 1920—1928), kde také zemřel.

Recenzovaná kniha je vhodným vodítkem pro určování kvetoucích rostlin na úrovni čeledi v rámci celosvětovém a jako takovou příručku ji možno doporučit všem, kdo potřebují určovat zcela neznámý materiál. Může být však také využita i pro úpravu určovacího klíče čeledí naší flóry.

J. Holub