



Review on infection biology of uromyces species and other rust spores

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ABSTRACT

Uromyces fabae (*Uromyces viciae-fabae*) the pea rust was first reported by D. C. H. Persoon in 1801. Later DeBary (1862) changed the genus and renamed it as *Uromyces fabae* (Pers) deBary. There after, Kispatic (1949) described *f. sp. viciae-fabae* by including host *vicia fabae*. The pathogen *Uromyces fabae* described as autoecious rust with aeciospores, urediospores and teliospores found on the surface of host plant (Arthur and Cummins, 1962; Gaumann, 1998). Gaumann proposed that the fungus be classified into nine *forma speciales* each with a host range limited to two or three species. Later it was observed that the isolates of *Uromyces viciae-fabae* share so many hosts in common that it was impossible to classify them into *forma speciales* (Conner and Bernier, 1982). Based on the distinctive shape and dimensions of substomatal vesicle, *Uromyces viciae fabae* has been described as a species complex (Emeran *et al.*, 2005). It revealed that host specialized isolates of *Uromyces viciae fabae* were morphologically distinct, differing in both spore dimensions and infection structure.

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Introduction

Uppal (1933) and Prasada and Verma (1948) found that several species of *Vicia*, *Lathyrus*, *Pisum*, and Lentil are susceptible to *Uromyces fabae* in India and abroad. In India species of *Vicia*, *Lathyrus* and *Pisum* are described as host plant for *Uromyces fabae* (pers) deBary, (Kapooria and Sinha, 1966; Kapooria and Sinha, 1971).

They recorded natural infection on *Vicia sativa* L. and *V. hirsuta* Gray, common weeds found in the field of lentil in India also. *Viciae faba* L., *V. biennes* L., *V. hirsuta*, and *V. arborensis* L. were described as highly susceptible to *Uromyces fabae*, *Viciae sativa* and *Lathyrus aphaca* were found to be disease free. Conner and Bernier (1982) reported a total of 52 species of *Viciae fabae* and 22 species of *Lathyrus* to be infected by *Uromyces viciae fabae*. They also found this pathogen on pea, lentil and *fababean*. Butler (1912) reported the occurrence of rust pathogen (*Uromyces fabae*) on pea and other leguminous crops from India.

Distribution

There were reports on occurrence of *Uromyces fabae* from most of the place in India. Butler (1912) reported this fungus from state of Maharastra. Pea rust (*Uromyces fabae*) is of world wide occurrence and attacks number of host species belonging to different genera of family leguminoseae in the Indo-gangetic plains Butler (1918) and Prasada & Verma (1948) also reported the occurrence of *Uromyces fabae* on lentil crops from Delhi. Roy (1949) in his list of fungi of Bengal recorded the prevalence of *Uromyces fabae* on the leaves and stems of *Pisum sativum*. Mitter and Tandon (1930), Patel (1943), Pavgi and Upadhyay (1966) and Kapooria and Sinha (1966) reported the distribution of this pathogen in the regions of Uttar Pradesh. Bilgrami *et al.*, (1979) reported the occurrence of this pathogen on various host species of pea, lathyrus and lentil. Baruah *et al.*, (1979) reported on the pea plants caused by both *U. fabae* and *U. pisi* is of rare occurrence in India. Occurrence of *U. fabae* is also available the rus from Canada (Conner and Bernier, 1982; Xue and Warkentin, 2002).

Variability in the pathogen

Pathogenic variability has been reported in field collection of *Uromyces fabae* (Singh and Sokhi, 1980; Conner and Bernier, 1982; Xue and Warkentin, 2002). The urediospores of *Uromyces fabae* were the infective spore and used in various resistance screening programme in pea (Xue and Warkentin, 2002); faba bean (Sillero *et al.*, 2000); lentil (Chauhan *et al.*, 1966) and sweet pea (Sokhi, 1984).

Mode of survival of the pathogen.

The aeciospores and urediospores of *Uromyces fabae* did not survive at temperature more than 30°C for one week; therefore, they were not supposed to survive at high temperature of the intervening crop season. Teliospore survives the intervening season and germinates to produce basidiospores Pycnia, developed from growth of basidiospores subsequently caused infection in pea (Singh, 1999). Conner and Bernier (1982) have suggested the role of collateral host in the recurrence of disease. They reported that *Vicia* species and *Lathyrus* species served as a collateral host to *Uromyces fabae* and helped in its survival during the absence of the main crop.

Infection process of rust fungi

Attachment of rust spores in host surface

Deising *et al.*, (1992) observed that the urediospores of rust fungus form adhesion pad release a cutinase and two specific esterases after contacting the host cuticle, apparently adhesion of the pad is improved by these enzymes Cutinase/esterase inhibitors altered this pattern of adhesion.

Hickman and Epstein (1988) has been described adhesion of fungal propagules to plant or artificial modal surface. Nicholson and Epstein (1991) analyzed chemical on polysaccharides, protein or glycoprotein. Beckett *et al.*, (1990) and Read *et al.*, (1992) found germtube of *Puccinia hordei* when fractured away from the barley cuticles, wax crystals adhered tightly to be underside of the germtube.

Germination of aeciospores

Hiratsuku and Powell (1966) studied the germinating aeciospores in case of *P. harknessii* and *P. stalactiforme* and

Found that binucleate spores of *P. stalactiforme* gave rises to nonseptum germtube with two nuclei. Meinecke, (1929) and Nighswander (1963) have noted that binucleate spores produced hyphae had one nucleus per cell. A similar observation was made by True (1939) for the woodgate rust fungus *P. harknessii*. Joseph and Hering (1996) reported that urediospores of *U. viciae-fabae* (Broad bean rust) germinated well in the range 5-26 °C, fastest germination at 20 °C exposure to 30 °C gave poor germination and damaged the spores. Joseph and Hering (1996) also reported that at 20°C some infection occurred within 4 hours leaf wetness, but longer wetness periods up to 24 hours gave increased infection. Relative humidity of 100% was favorable for aeciospores germination while 98% RH favoured urediospores germination (Kushwaha and Chand 2006). Maximum germination 2% was observed at 25°C.

Appressorium formation

Maheswari *et al.*, (1967) reported that heat shock induced the formation of appressorium. Davies and Butler (1968) and Mendgen (1973) reported that appressoria attach firmly to their substrates by means of extracellular adhesives or above stomatal pores appressoria of many rust fungi get by wedging their base between the outer edges of the stomatal opening. Macko *et al.*, (1978) and Grumbow (1977) found chemical stimuli include metabolites extracted from urediospores, for appesoria formation. Kaminsky and Day (1984) reported that ions like K⁺⁺ and Ca⁺⁺, sucrose also acts stimuli for appressorium development. Hoch and Staples (1984) reported that cyclic nucleotides or stimulators of adenylates cyclase also responsible for appressorium formation. Gold and Mendgen (1984) observed that basidiospores of *Uromyces appendiculatus* penetrates mostly from appressoria, but some times penetrates directly with very short germtube. Kapooria and Mendgen (1985) reported that the uredosporelings of *U. appendiculatus*, *U. viciae-fabae*, *Phakopsora packyrhizi* and aeciosporelings of *Arthuriomyces peckianus*, nuclear division was strictly correlated with appressorium development including septum formation. Hoch *et al.*, (1987) reported that topographical signals such as scratches or precisely defined ridges on a membrane also induce the formation of appressorium. Bourette and Howard (1990) reported that fungi recognized physical differences in topography and rigidity of the substrates before appressoria formed. Kwon and Hoch (1991) reported that the germtube of *U. appendiculatus* senses inductive topographies such as stomatal opening or a precisely defined ridges of 0.5 µm height over which the appressorium will be positioned within 4 minutes of initial contact. Bourette and Howard (1990), Kwon and Hoch (1991) reported *U. appendiculatus* and *M. grisea* need only 40-50 minutes to form a septum that delineates the appressorium. Read *et al.*, (1992) reported that the mechanism by which a hyphal tip could sense minute surface features may includes the different components of the cytoskeleton or an ionic or electric changes mediated by mechanosensitive channels. Bourette and Howard (1991) and Kwon *et al.*, (1991) also reported that the substrate, microtubules and microfilaments were arranged in a reticulate pattern, close to appressorial wall, with peripheral plaques adjacent to the plasma membrane. Deising *et al.*, (1991) reported that appressoria detach easily from their substrates if they are produced on artificial membranes because the infection peg was able to lift the appressorium from the substrates. Mims and Dyke (1991) reported that appressoria of uredosporelings from rust fungi penetrate through stomata. Swann and Mims (1991) also studied that there were many fungi that penetrate the epidermis directly without producing appressorial cones. Chand and

Kushwaha (2006) observed that only about 1% of germling formed appressorium, but most of the appressorium were found away from stomata.

Penetration hypha

Chang *et al.*, (1981) reported that monokaryotic hypha of rust fungi was constricted during penetration, but fungal wall did not exhibit obvious specialization during penetration of the host wall. Koch *et al.*, (1983) reported that rust fungus in dikaryotic stage, developed appressoria and a penetration hypha. Gold and Mendgen (1984), Mims and Richard (1989) reported monokaryotic, appressoria were basely developed and the penetration hypha was specialized. Harder and Chang (1991) found very specialized haustoria mother cell during intercellular growth.

Host surface penetration

Xu and Mendgen (1991) found that basidiospores of *U. vignae* can penetrate the host cuticle of *Vicia faba* much faster and with higher efficiency then the host epidermis, but the infection was stopped a few hours later within the cytoplasm. Heiler *et al.*, (1993) reported that the uredosporelings of *Uromyces viciae-fabae* produced a cellulolytic enzyme that was regulated in a strickly differentiation in specific manners. Heiler *et al.*, (1993) reported that production of these enzymes continued during later stages of infection hypha when haustorial mother cells were formed.

Infection hypha and differentiation of hypha

Hoch and Staples (1983) observed that the endoplasmic reticulum appears more differentiated during growth (within the host plant) of germtube of *Uromyces appendiculatus*. Gold and Mendgen (1984) found that monokaryotic infections, by basidiospores of rust fungi produce a short germtube, modestly developed appressorium and a penetration hypha which elongates to form intraepidermal vesicles with a primary hypha.

Gold and Mendgen (1984); Freytag and Mendgen (1991) reported that the wall of infection hypha is quite thin and covered with a matrix. Ehrahim *et al.*, (1985) and Harder *et al.*, (1986) reported that the inner wall layer of infection hyphae of *P. packyrhizi*, *U. viciae-fabae*, and *P. graminis* has high affinity to WGA.

Welter *et al.*, (1988) found tubular vesicular complex in intercellular hyphae and in haustoria. Health (1988) reported that infection starting from basidiospores of *Uromyces vignae* induces hypersensitive cell death as soon as they penetrate epidermal cells of an incompatible host plant. Boller and Metraux (1988) reported that Mannoprotein may cover the chitin and make the wall resistance to further attacked by chitinase and beta-1, 3-glucanases occurring in leaf apoplast. Mims *et al.*, (1989) found inner layer of infection hyphae of *P. arachidis* was covered with additional easily discernible coatings.

Grignon and Sentenao (1991) reported that the physiochemical properties of the cell wall degrading enzymes of *Uromyces viciae-fabae* may be of critical importance in avoiding extended tissue damage and thus for establishment of biotrophy since pH of the apoplast was in weakly acidic range pH (5 - 6.5). Frittrang *et al.*, (1992) reported that in the biotrophic fungus *U. viciae-fabae*, pectin esterase isoenzymes have been separated by chromatofocusing and these forms of enzymes, showing pH of 8.4, 5.7 and 4.7 were detected 9 hours after inoculation when young hypha was formed. Heiler *et al.*, (1993) reported that at the stages of infection hypha differentiation activity of neutral cellulases increased dramatically and this increase continued until haustorial mother cell formed.

Haustorial formation

Borland *et al.*, (1980) studied the diameter of aecial haustorium at the site of host wall penetration was greater than telial haustorium, and aecial haustorium was hyphal in appearance while the telial haustorium posses a slender neck region with darkely staining neck band a lobbed haustorial body. The aecial haustorium characteristically possesses a septum near its proximal end while such a septum was absent from telial haustorium. Voegelé *et al.*, (2001) reported that fungal biotrops differentiate specialized infection structures within the living cells of their host there haustoria have been linked to nutrient uptake ever since their discovery. uptake sugars from the host (*Vicia fabae*) to the rust fungus (*Uromyces fabae*) seems to be occurred largely through haustorial complex. Quilliam and Shattock (2003) reported that *Uromyces ficariae* (microcyclic) and *U. dactylidis* (macrocyclic, heteroecious) both produced vermiform and largely indeterminate intracellular hyphae typical of M- haustoria associated with telial and aecial galls, respectively on their common host *Ranunculus ficaria*. Similar M-haustoria were observed in telia galls of *Puccinia tunida* (microcyclic) on *Conopodium nrajus* in host tissue affected by nine other microcyclic spp and in aecial galls of *P. smyrni* (demicyclic, autoecious) on *Smyriniu alusatrum*. To identify gene expressed during biotrophic growth, EST sequencing was performed with a haustorium cDNA library from *Uromyces fabae*.

Development of aecium cup

Orientation of aecium cup

Spiers and Hopcraft (1985) first indicated aecial development was the formation of rows of vertically orientated club-shaped cells within mesophyll tissue. These elongated and divided forming a single terminal peridial cell and an intercalary cell, which later broke down. Peridial cells thus formed a protective layer over underlying aeciosporophores. Developing columns of aeciospore initials later obscured all evidence of peridial cell formation. Peridial cells were dikaryotic and were readily distinguished from aeciospores by their solitary nature and dagger-like ornamentation. These aecia were subepidermal and developing aeciospores were covered with single layer of dikaryotic peridial cells. Aeciospores formation was meristem arthosporic. Aeciospores were globose to subglobose and verrucose with cog like knobs superficially embedded in the secondary cell wall reported in *Melampsora larici*

Formation of peridium layer

Rijkenberg and Truter (1974) reported sporogenous cell or aeciosporophores of aecium eventually formed at the base of aecial primordium and appear to arise from large multinucleate cells. The sporogenous cells produced in this way each contain two nuclei that divide conjugately during formation of aeciospores initials two of the daughter nuclei remain in the sporogenous cell while the other two move into aeciospore initial. After the initial is delimited from the mother cell by a septum, the nuclei in the initial divide again and a transverse septum separates the initial into binucleate aeciospores and a small wedge-shaped, binucleate, sterile, intercalary or disjunct cell (Rijkenberg and Truter, 1974). In most of species of rust fungi the peripheral cells of aecial base undergo successive divisions to produce a wall that surrounds the spore chains. Peterson (1974) reported that aecia of *M. medusae* and *M. pinitorque* were peridiate. Wilson and Henderson (1966) reported that there was no evidence for the peripheral paraphyses like hyphae neither united to form a rudimentary peridium nor were peridia formed as early products of basal cells which later formed

aeciospores as speculated for *Melampsora* species by (Peterson, 1974).

Formation of aeciospores chain

Hughes (1970) reported that aeciospores were meristem arthosporic. Rijkenberg and Truter (1974) reported that aeciospores are not annellophoric in *P. sorghi* and also reported that cell analogous to the multinucleate fusion cell was observed in the base of aecial stroma.

However, in *M. epitea* and *M. larici-populina* the cell were less extensive than those of *P. sorghi*. Rijkenberg and Truter (1975), Littlefield and Heath's (1979) reported that aeciospores ornamentation developed as outerlined. Holm and Tibbell (1974), Moore and McAlear's (1961) studied the verrucose aeciospores of *M. epitea* and *M. larici-populina* with their cog like knobs were similar to those of *P. recondata*. Gold and Littlefield (1979) reported that aeciospores of *M. lini*, in contrast, were coarsely verrucose and spine were wart-like.

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