Puccinia

Systematic Position

Kingdom	—	**Mycota**
Division	—	**Eumycota**
Sub-division	—	**Basidiomycotina**
Class	—	**Teliomycetes**
Order	—	**Uredinales**
Family	—	**Pucciniaceae**

Puccinia is a very large genus with about 1,800 species, practically distributed in all parts of the world. In India, the genus is represented by more than 147 species, which cause serious rust diseases in cereal crops like wheat, barley, oats and maize. The species of *Puccinia* are internal obligate parasites; only spores are seen on the host surface. Obligate parasites can not be grown on artificial culture medium, but Williams (1966), Heifer (1989) and others have been successful in growing some species of *Puccinia* (e.g., *P. coronata, P. hordei, P. recondita, P. striiformis, P. graminis tritici*) on culture medium.

Species of *Puccinia* may be autoecious, i.e., they complete their life cycle on a single host (e.g., *P. asparagi, P. butleri, P. menthae, P. pulverulenta*), or heteroecious, i.e., they complete their life cycle on two different hosts (e.g., *P. graminis, P. coronata*).

In India, wheat crop is infected by the following three species of *Puccinia* which cause considerable damage to the crop.

(1) *P. graminis* — black rust or stem rust.
(2) *P. striiformis* (= *P. glumarum*) — yellow rust or stripe rust.
(3) *P. recondita* (= *P. tritici*) — brown rust or leaf rust.

Distinguishing features of these three species are listed in Table 1.

Puccinia graminis

Puccinia graminis is the causal organism for **black rust** disease of wheat and other cereal crops. This disease is also known as **stem rust**. The pathogen responsible for the disease was earlier considered to be an insect, but Persoon (1797) for the first time reported that the disease is caused by a fungus. *P. graminis* is an obligate parasite. It is a **heteroecious** fungus. There are two phases — **dikaryophase** and **haplophase** — in its life cycle. The dikaryophase occurs in its primary host, wheat (*Triticum aestivum*), whereas the haplophase in its alternate host, *Berberis vulgaris*. Although *P. graminis* can survive in the absence of alternate

***Table 1.* Distinguishing features of *Puccina graminis*, *P. striiformis* and *P. recondita*.**

P. graminis	*P. striiformis*	*P. recondita*
1. Causes **black rust** disease in wheat.	Causes **yellow rust** disease in wheat.	Causes **brown rust** disease in wheat.
2. Appears in March in northern India and in the last week of November in South India.	Appears in January-February in northern and eastern India.	Appears in January in northern and eastern India.
3. Uredosori appear mainly on stems but in later stages leaves and ears are also infected.	Uredosori mainly appear on leaf-sheaths and ears.	Uredosori are confined to leaves.
4. Uredopustules are large, elongated and red or brown in colour.	Uredopustules are small, oval and are arranged in long strips.	Uredopustules are small, oval or round, scattered and bright orange.
5. Uredospores are oval and brown with 4 round equatorial germ pores.	Uredospores are nearly round and yellow with 6-10 scattered germ pores.	Uredospores are round or oval and bright orange with 3-4 germ pores.
6. Teleutosori are elongated and black in colour; they are confined to the stem.	Teleutosori form black elongated pustules; they are confined to the lower surface of the leaf.	Teleutosori rarely develop; if present, they are black and are confined to the lower surface of the leaf.
7. Telia burst on maturity.	Telia donot burst.	Telia donot burst.
8. Teleutospores are bi-celled, chestnut brown to black; round or conical at the apex.	Teleutospores are bi-celled, cuniform and constricted at the septum; conical at the apex.	Teleutospores are bi-celled and dull black; rounded and thickened at the apex.
9. The alternate host is *Berberis vulgaris*.	The alternate host is *Muehlenbergia hugeli*.	The alternate host is *Thalictrum falvum*.

host, its life-cycle is completed only when both hosts are available.

Physiological Specialization

Puccinia graminis has several physiological races, which show physiological specificity towards their hosts. For instance, *P. graminis* causes rust disease in several cereal crops like wheat, barley and oats, but the strain which infects wheat plants does not infect barley or oats. This is due to the fact that each strain has some metabolic specificity towards the host. The phenomenon where a specific host is infected by a specific pathogen is called **biological specialization**.

P. graminis is thus a composite species. On the basis of its pathogenecity, size of uredospores and cultural variability it has been divided into the following six strains.

Strain	Host
(1) *P. graminis tritici*	Wheat
(2) *P. graminis secalis*	Rye
(3) *P. graminis avenae*	Oat
(4) *P. graminis phleipratensis*	*Festuca*
(5) *P. graminis agrostis*	*Agrostis*
(6) *P. graminis poae*	*Poa*

Each strain has several physiological races. For example, about 300 physiological races of *P. graminis tritici* have already been isolated.

In India, wheat crops in northern and southern regions are largely affected by *P. graminis*. The rust usually appears late in the season. It is often not seen in northern India until March, the earing time of the crop. However, in south India the disease appears in November and as such the vegetative growth of the crop is most affected. The infection decreases the rate of photosynthesis, causing a great loss to yield.

Vegetative Structure

There are two types of mycelia — dikaryotic and monokaryotic — in the life-cycle of *P. graminis*. Both these mycelia are intercellular, septate and branched. There is a simple pore in each septum which maintains protoplasmic connections between the adjacent cells. The cell wall is composed of chitin and glucan.

The dikaryotic mycelium occurs in the primary host, i.e., wheat plants, whereas the monokaryotic mycelium occurs in the alternate host, i.e., barberry bushes. Each cell of the dikaryotic mycelium has a dikaryon and that of monokaryotic mycelium a single nucleus. The granular cytoplasm of the cell also contains vacuoles, glycogen bodies and oil globules. The mycelium takes nourishment from the host cells with the help of spherical haustoria. The haustoria are often closely appressed to the nucleus of the host cell.

Life-cycle

Puccinia graminis is a macrocyclic heteroecious rust. There are five types of spores, viz., uredospores, teleutospores, basidiospores, pycnidiospores and aeciospores in its life cycle. These spores develop in two different hosts in a definite sequence. The sequence of various stages occurring in the primary and alternate hosts are as follows.

Uredospore stage Teleutospore stage	**on primary host** (*Triticum aestivum*)
Basidiospore stage	
Pycnidiospore stage Aeciospore stage	**on alternate host** (*Berberis vulgaris*)

A. Stages of *Puccinia graminis* on Wheat Plant

[I] Uredospore stage

The dikaryotic mycelium is produced by the germination of aeciospores on wheat plants. It enters through stomata and develops in the intercellular spaces in the tissues of the leaf, stem and glumes of the host. The dikaryotic mycelium, present in the sub-epidermal region, develops many erect hyphae which grow at right angle to the epidermis. A binucleate uredospore develops at the tip of each erect hypha (Fig. 1 B). These spores develop in groups and these groups are known as **uredosori**. With the formation of uredospores, disease symptoms appear in the form of reddish-brown pustules or streaks on the stem, leaf and leaf base (Fig. 1 A). These symptoms usually appear in late spring. The host epidermis bursts due to the pressure of developing uredosori and thus uredospores are liberated.

The mature uredospore is a stalked, unicellular, oval and binucleate structure (Fig. 1 C). The spore wall is thick and is differentiated into three layers;

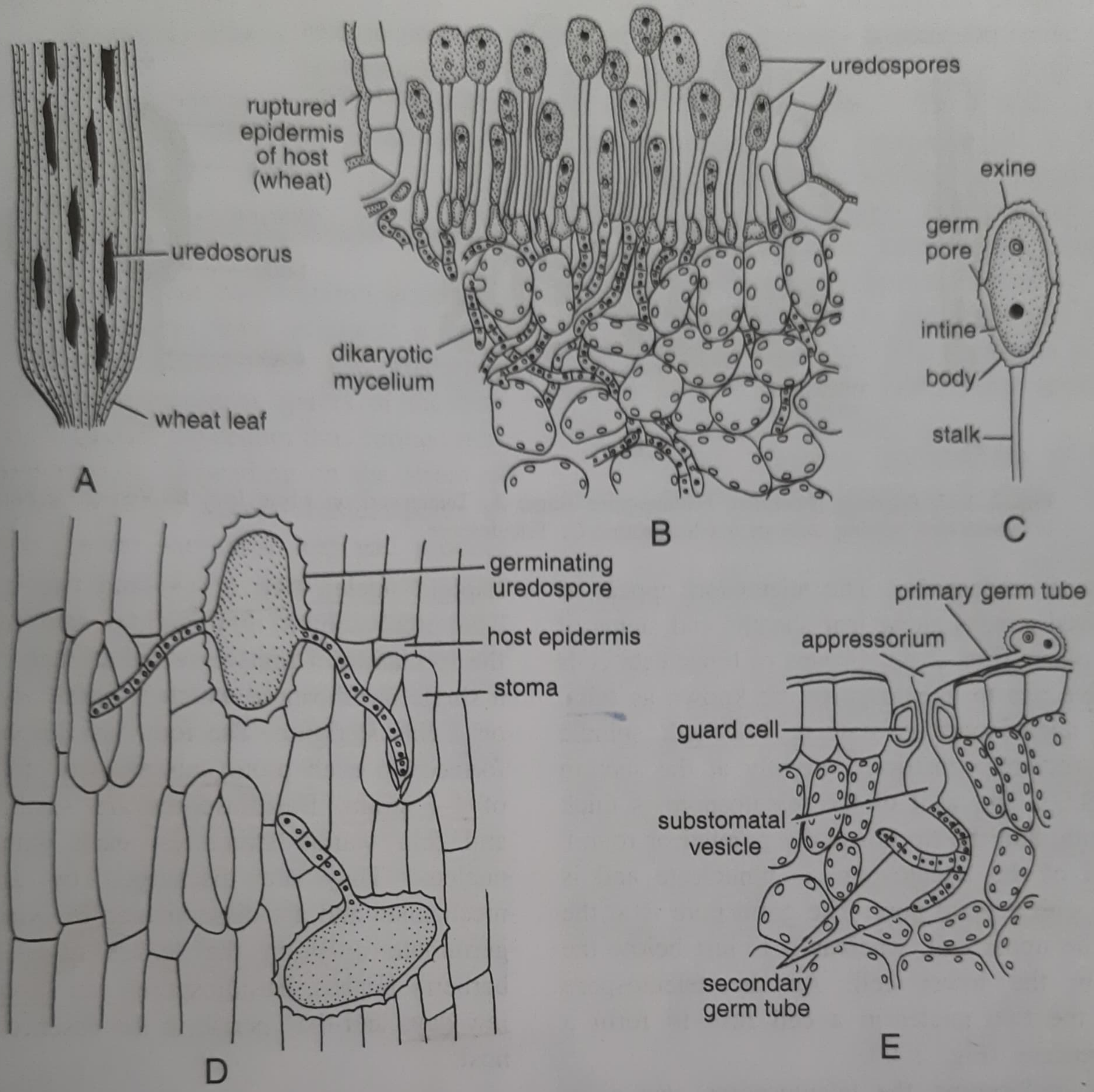

Fig. 1 A-E. *Puccinia graminis*: Uredospore stage; A. Uredosori on wheat leaf, **B.** Vertical section of wheat leaf passing through a uredosorus, **C.** A uredospore, **D, E.** Germination of uredospores.

the outer layer is relatively thick and spiny, whereas the inner layer has four equatorial thin areas, called **germ pores**.

The binucleate uredospore functions as a conidium and it has the capacity to germinate immediately after its formation. Uredospores can reinfect wheat plants and hence they are effective in the spread of the disease. However, they are incapable to infect the alternate host, barberry bushes.

Germination of uredospores. Under favourable conditions, uredospores germinate as soon as they come in contact with fresh wheat leaves. Each produces one or more germ tubes through germ pores. The germ tube grows over the surface of the host epidermis and on reaching a stoma the tip of the germ tube develops into a vesicle, called appressorium. Hyphal branches develop from the appressorium in the intercellular spaces (Fig. 1 D, E). This dikaryotic mycelium forms a new generation of uredospores which infect healthy plants. This results into a heavy build up of infection on wheat crop. Once formed, the uredospores spread the disease rapidly under favourable conditions.

[II] Teleutospore stage

At the close of the wheat season, the uredosori also start producing teleutospores in addition to uredospores. The uredosori are ultimately converted into teleutosori and produce teleutospores exclusively. Teleutosori are also produced independently from the mycelium formed by the late

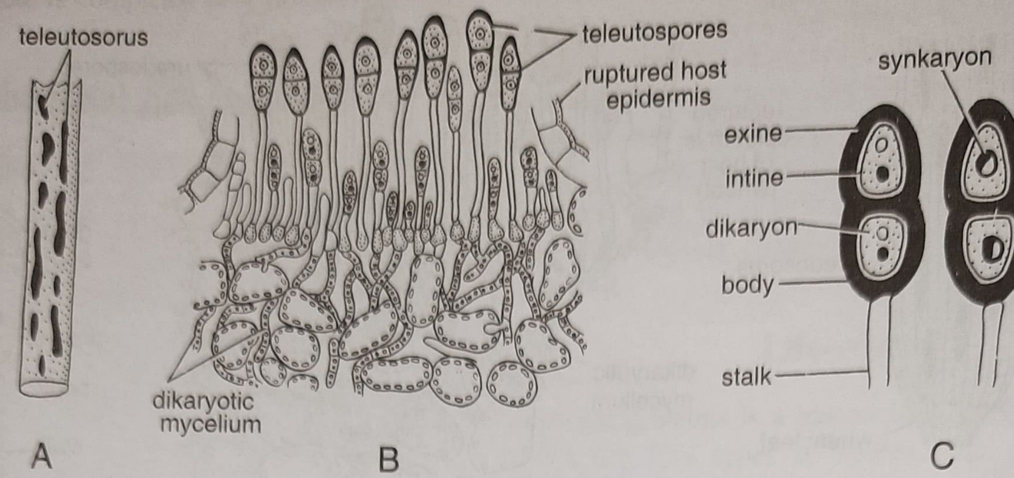

Fig. 2 A-C. ***Puccinia graminis*****: Teleutospore stage; A.** Teleutosori on wheat leaf, **B.** Vertical section of wheat leaf passing through a teleutosorus, **C.** Teleutospore.

infection of uredospores. The teleutosori appear as black raised streaks along leaf sheaths and stems of infected plants (Fig. 2 A). Groups of binucleate cells which give rise to teleutospores are known as **telia**.

The teleutospore is stalked, bi-celled, spindle shaped structure, constricted slightly at the septum (Fig. 2 B,C). The wall of the teleutospore is thick and smooth, and the tip is usually pointed or round. Each cell of the teleutospore is binucleate and is provided with a germ pore. The germ pore is at the apex in the upper cell, whereas it is just below the septum in the lower cell. As the teleutospore matures, the two nuclei in a cell fuse to form a diploid nucleus (Fig. 2 C).

Like uredospores, the teleutospores also exert pressure on the overlying epidermis. The epidermis is thus ruptured and the spores are exposed. The teleutospores act as resting spores and may survive most unfavourable conditions. They are incapable of reinfecting wheat plants. They do not germinate until the next spring. Under favourable conditions of high atmospheric humidity and low temperature, they germinate in soil as no host is required for their germination.

[III] Basidiospore stage

On return of favourable conditions in spring, the teleutospore germinates. It produces one germ tube from each cell. The germ tube has limited growth and is known as **promycelium** or **epibasidium** (Fig. 3 A, B). The diploid nucleus moves into the promycelium and divides meiotically to form four haploid nuclei, two of (+) and two of (–) strain. The promycelium now divides into four cells by the formation of transverse septa. Each cell produces a single basidiospore which is borne asymmetrically on a fine sterigma. The four basidiospores are thus formed on each promycelium, two of (+) and two of (–) strain. Basidiospores are small, unicellular and thin walled structures, each with a haploid nucleus. They are discharged by an explosive mechanism and are disseminated by wind. They can germinate only on the leaves of alternate host, barberry bushes. Basidiospores can survive only for few days and they perish in the absence of alternate host.

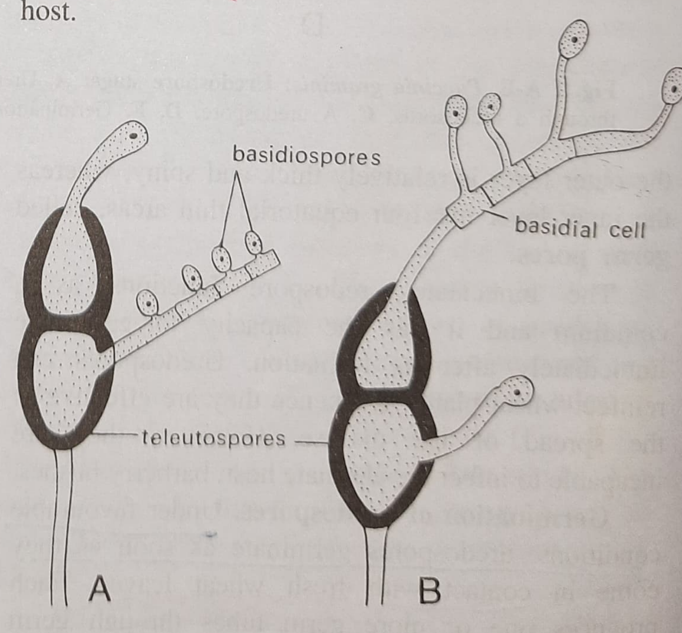

Fig. 3 A-B. ***Puccinia graminis*****:** Germination of teleutospore and formation of basidia.

B. Stages of *Puccinia graminis* on *Berberis* Plant

The haplophase of *P. graminis* occurs on *Berberis* plant. This phase begins with the formation of basidiospores.

[I] Pycnidiospore or spermogonium stage

Under favourable conditions basidiospores germinate on the leaves of *Berberis*. Each produces a germ tube which penetrates through the leaf epidermis and grows into the intercellular spaces of the host tissue. The monokaryotic mycelium thus formed may be of (+) or (–) strain, depending on the strain of the basidiospore. Usually several basidiospores of different strains infect the same leaf and produce mycelia of both (+) and (–) strains. After a few days of infection the mycelia become aggregated into pseudoparenchymatous masses beneath the leaf epidermis and form spermogonia or pycnidia. The spermogonia are yellowish flask-shaped structures, developed on the upper surface of the leaf. They may be of (+) or (–) strain, depending on the strain of the mycelium. The spermogonium opens on the upper surface of the leaf by a minute pore, called **ostiole**. The ostiole is guarded by a tuft of unbranched, tapering, orange-coloured sterile hairs, known as **periphyses**. Amongst the periphyses thin-walled branched **flexuous hyphae** (receptive hyphae) are also present and these hyphae project much beyond the periphyses. The wall of the spermogonium is lined internally with a palisade-like layer of numerous, uninucleate tapering cells, known as **spermatiophores** (pycniophores). Each spermatiophore abstracts many small, uninucleate spermatia (pycniospores). Spermatia ooze out through the ostiole and are held by the periphyses in sticky drop of liquid (Fig. 4 B). The spermatia are small, oval to spherical, hyaline and smooth spores. They may be of (+) or (–) strain.

There are numerous spermogonia of both (+) and (–) strains on the leaves of *Berberis*. Spermatia can neither infect the primary host nor the alternate host. When spores are released, the spermogonium secretes nectar drops which attract insects. The spores of one strain are transferred to the flexuous hyphae of the opposite strain by insects. This process is known as **spermatization**. At the point of contact of spermatium with the flexuous hypha the walls are dissolved and the nucleus of the spermatium is transferred to the flexuous hypha. A dikaryotic mycelium is formed as the result of spermatization. During the course of spermogonial formation, some hyphae of each mating type form **protoaecidia** on

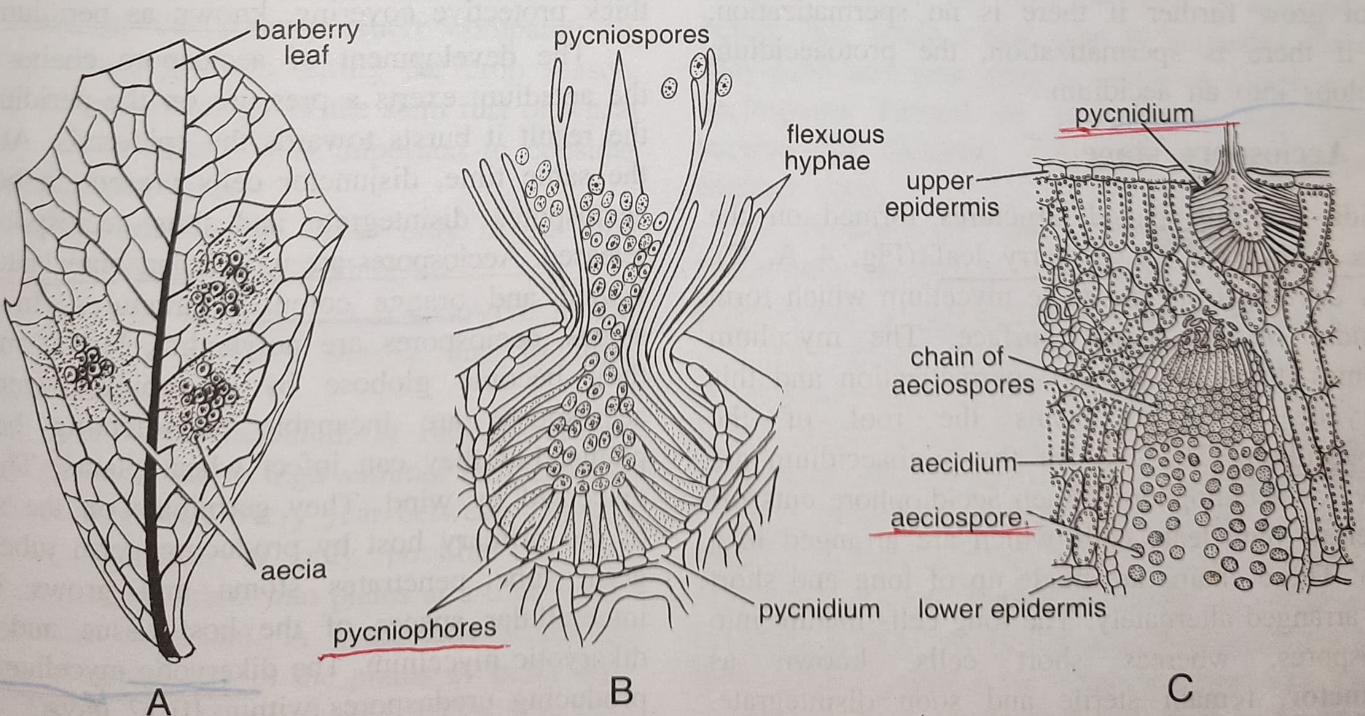

Fig. 4 A-C. ***Puccinia graminis*: Spermogonium and aeciospore stage; A.** Aecidium on the lower surface of *Berberis* leaf, **B.** Longitudinal section, **C.** Vertical section of a leaf to show a young pycnidium (upper surface) and a mature aecidium (lower surface).

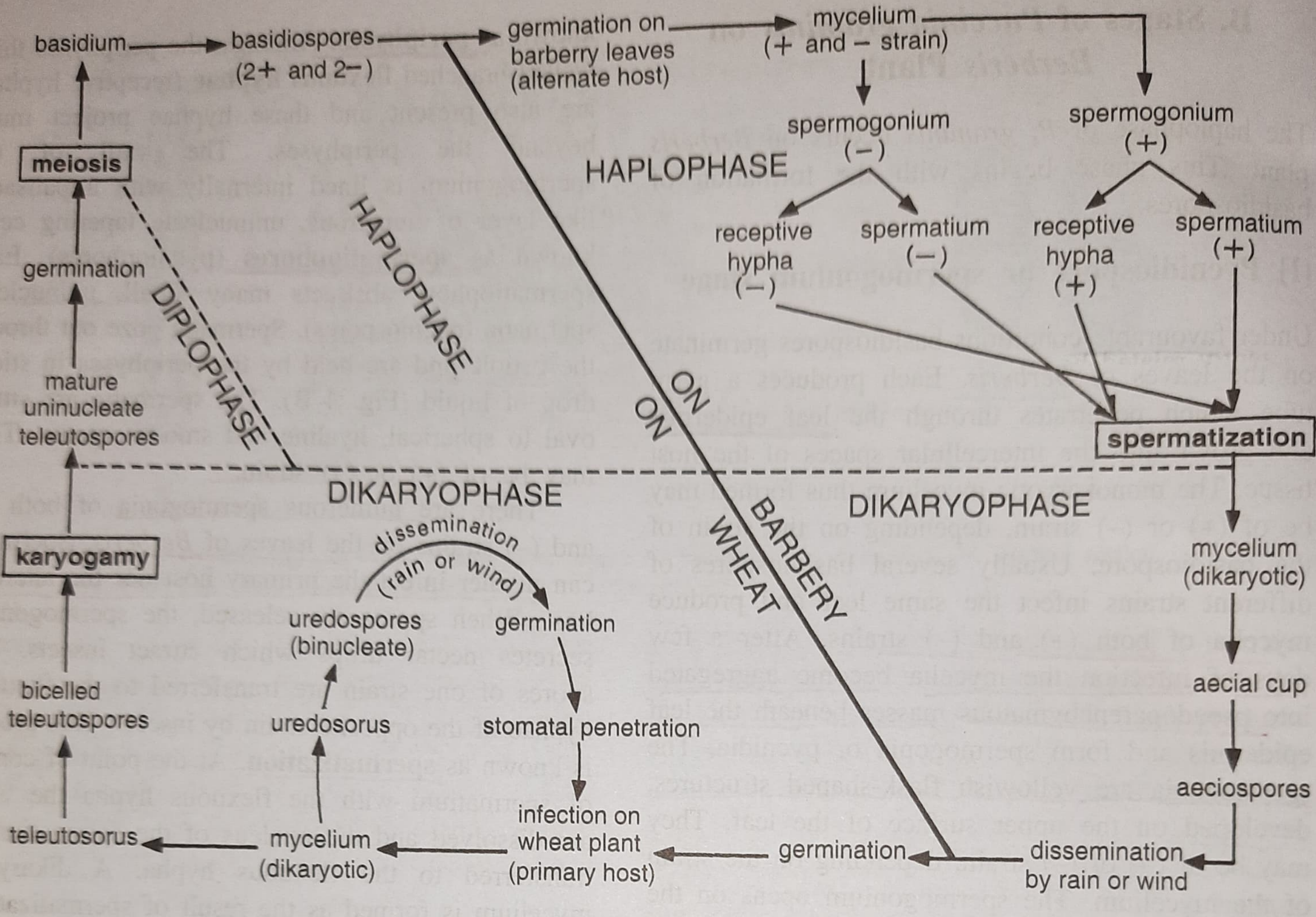

Fig. 5. ***Puccinia graminis***: Schematic representation of the life-cycle.

reaching the lower surface of the leaf. The protoaecidia appear as globose mass of hyphae. They donot grow further if there is no spermatization, but if there is spermatization, the protoaecidium develops into an aecidium.

[II] Aeciospore stage

Aecidia are cup-shaped structures formed on the lower surface of the barberry leaf (Fig. 4 A, C). They develop from the same mycelium which form pycnidia on the upper surface. The mycelium becomes dikaryotic due to spermatization and this dikaryotic mycelium forms the roof of the protoaecidium. The cells of the protoaecidium are known as aecidiophores. Each aecidiophore cuts off numerous binucleate cells which are arranged in a chain. These chains are made up of long and short cells arranged alternately. The long cells mature into aeciospores, whereas short cells, known as **disjunctor**, remain sterile and soon disintegrate.

Simultaneously with the formation of aeciospores, the peripheral cells of aecidium divide to form a thick protective covering, known as peridium.

The development of aeciospore chains inside the aecidium exerts a pressure on the peridium. As the result it bursts towards the epidermis. At about the same time, disjunctor cells present in between aeciospores disintegrate and thus aeciospores are released. Aeciospores are unicellular, binucleate, thin-walled and orange coloured structures. In young stages, aeciospores are polyhedral, but at maturity they become globose by absorbing water. The aeciospores are incapable of infecting barberry plants, but they can infect wheat plants. They are dispersed by wind. They germinate on the surface of the primary host by producing germ tubes. The germ tube penetrates stoma and grows in the intercellular spaces of the host tissue and forms dikaryotic mycelium. The dikaryotic mycelium starts producing uredospores within 10-12 days.