

REVIEW

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The diversity of nuclear cycle in microcyclic rust fungi (Uredinales) and its ecological and evolutionary implications

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Abstract Nine types with 11 variations of nuclear cycle and associated metabasidium development were distinguished in microcyclic rust fungi. An additional type was recognized in rust fungi with an expanded life cycle. A significant proportion of rust fungi with a reduced life cycle is assumed to have lost a sexual genetic recombination process, being either apomictic or asexual in reproduction. Most species that retain a sexual process in the microcyclic life cycle seem to have become homothallic. During life cycle evolution by the omission of spore stages, these traits might have had a selective advantage for those species that had less opportunity to encounter a genetically different but sexually compatible mate because of isolated patchy distribution or a short growing season. The findings that different populations of a morphologically identifiable species exhibit two or more distinct patterns of nuclear cycle and different metabasidium development indicate that microcyclic lineages might have evolved independently and repeatedly from a macrocyclic parental species. Those lineages are morphologically the same but would differ from each other in their genetics and biology.

Key words Basidiospore · Ecology · Evolution · Life cycle · Metabasidium

Introduction

The rust fungi (Uredinales, Basidiomycota) consist of 6929 species in 163 genera in 14 families and comprise approximately 10% of all described and named species in the kingdom Fungi (Kirk et al. 2001). The Uredinales has been believed to be a monophyletic taxon, and recent molecular phylogenetic analyses (Swann et al. 1998; Sjamsuridzal et al.

1999) support this perspective. A phylogenetic placement of families has not been critically evaluated, however (Swann et al. 2001). All the rust fungi are ecologically obligate parasites on ferns, gymnosperms, and angiosperms (perhaps on mosses as well). The parasitism of rust fungi to the host plant is highly specific. However, the degree of host specialization varies with species. Thus, some species are limited to a single species or a few closely related species in a genus or a few allied genera of a plant family. Others, e.g., *Phakopsora pachyrhizi* Syd. & P. Syd. and *P. meibomia* Arthur (Ono et al. 1992), occur on a large number of species in several genera of the plant family Leguminosae. Only a limited number of species have been axenically cultured on semidefined media (MaClean 1982).

Besides the characteristic nature of obligate parasitism on vascular plants, rust fungi are unique in having complex life cycle patterns with elaborate spore forms in the life cycle stages. Rust fungi produce up to five distinct spore forms in respective stages of the life cycle. Accordingly, the life cycle may be composed of spermogonial, aecial, uredinial, telial, and basidial stages. This life cycle is said to be macrocyclic. When all the stages are produced on plants of a single species or closely related species, the life cycle is called autoecious. On the other hand, when spermogonial and aecial stages occur on plants of a group of species and uredinial and telial stages on a different group of host plants, the life cycle is called heteroecious. The spermogonial aecial host(s) and the uredinial telial host(s) are eco-geographically closely associated. They are phylogenetically distantly related, however. The heteroecious life cycle is widespread in the Uredinales, whereas the mode of life cycle similar to heteroecism has been reported only in a few species of *Ceolomyces* (Blastocladales, Chytridiomycota) (Whisler et al. 1974, 1975) and in *Pyxidiophora* (Laboulbeniales, Ascomycota) (Blackwell and Malloch 1989).

A life cycle is said to be macrocyclic when all spore forms are produced in a unidirectional order in the life cycle. In the demicyclic life cycle, the uredinial stage is omitted. When only a telial stage with or without a spermogonial stage is formed on a plant throughout the season, the life

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cycle is said to be microcyclic. In some species whose aeciospores are morphologically indistinguishable from urediniospores, their life cycle is called either macrocyclic or brachycyclic depending on the terminology and definition of spore stages. Terminology of spore forms and life cycle has been discussed by Arthur (1925), Hiratsuka (1973a,b, 1975, 1991), Hiratsuka and Sato (1982), Holm (1973, 1984, 1987), Laundon (1967, 1972), and Savile (1968, 1988). The ontogenic system of terminology (Hiratsuka 1973a, 1975) is employed throughout this article.

The complex life cycle with elaborated spore forms produced in each stage and the obligate parasitism of rust fungi have long drawn the attention of mycologists. The origin and evolution of obligate parasitism and the complex life cycle in rust fungi have been the subject of considerable debate, and a wide variety of hypotheses have been submitted for verification [Fitzpatrick 1918a,b; Orton 1927; Dodge 1929; Jackson 1931, 1944; Couch 1937, 1938; Linder 1940; Stanley 1940; Leppik 1953, 1955, 1956, 1959, 1961, 1965, 1967, 1972, 1973; Savile 1955, 1976; see Hennen and Buriticá (1980) and Petersen (1974) for a brief review]. Currently, there is no universally accepted theory to reasonably explain this important subject, however.

A widespread assumption is that parasitism and host specialization were acquired at an early stage of the rust–fungus evolution. Speciation, ecophysiological diversification, and geographic distribution changes of host plants are believed to have played a vital role in the evolution and ecological diversification of rust fungi.

Thus, no matter which fungus, i.e., a *Herpobasidium*-related fungus parasitic on ferns (Jackson 1935), an auriculariaceous parasitic fungus related to *Jola*, *Eocronartium*, *Herpobasidium*, and *Platycarpa* (Leppik 1955, 1965), an ascomycetous proto-*Taphrina* parasitic on ferns (Savile 1955, 1976), or a *Pachnocybe*- or *Helicobasidium*-related fungus (Swann et al. 1998), was an immediate ancestor of rust fungi, the “first rust fungus” certainly possessed only a basidial stage with morphologically undifferentiated probasidia (teliospores). The life cycle of the ancestral rust fungus only with the basidium stage is said to be “unexpanded” (Hennen and Buriticá 1980). From this ancestor, progenies have evolved through jumping to other plants and entering different environments, particularly with seasonally changing climates. The life cycle might have expanded with the addition of vegetative spore forms (aeciospores and urediniospores) and sex-related structures (spermogonia), as depicted by Jackson (1931) and Hennen and Buriticá (1980).

Through the process of speciation and concomitant ecophysiological changes, which followed host speciation and their changes in ecogeographic distribution, some rust fungi might have reduced their life cycle by eliminating one or more spore stages. This evolutionary process of life cycle reduction ultimately resulted in rust fungi that produce only a telial/basidial stage in their life cycle. This life cycle is said to be reduced (Hennen and Buriticá 1980). During the reduction of life cycle in some, particularly heteroecious, species, the function of the telial stage was transferred to the aecial stage. This phenomenon has been explained un-

der “Tranzschel’s law.” The life cycle of those species that produce morphological aeciospores with the function of teliospores is called endocyclic, a special case of the microcyclic life cycle.

Consequently, those rust fungi that possess a microcyclic life cycle are of two groups with different evolutionary backgrounds, one retaining the most primitive trait and another the most advanced. Microcyclic species constitute a larger proportion of the rust biota in arcto-alpine regions (Arthur 1928; Hiratsuka 1935; Savile 1953) than in temperate regions. Endemic microcyclic rust fungi have also been found in oceanic islands (Hennen and Hodges 1981; Hodges and Gardner 1984; Gardner 1990, 1996). The life cycle of those species is considered to be reduced (Ono 2002). These arcto-alpine species are often isolated and patchy in distribution. In contrast, many tropical species producing only a telial stage are considered to be unexpanded in their life cycle (Hennen and Buriticá 1980; Ono and Hennen 1983; Ono 2002). Hereafter, the term microcyclic refers to a life cycle that has been reduced to form only the telial stage.

Rust fungi with a reduced microcyclic life cycle are most diverse in nuclear behavior and accompanying development of metabasidia and basidiospores (Walker 1928; Jackson 1931; Petersen 1974). A general tendency that microcyclic rust fungi with ecogeographically isolated distribution exhibit a wide variation in their nuclear cycle implies the evolutionary and ecological significance of life cycle reduction because the variation is likely to be associated with the loss of the sexual genetic recombination process.

Cytological studies of the rust life cycle have been reviewed by Moreau and Moreau (1919), Dodge and Gaiser (1926), Dodge (1929), Jackson (1931, 1935), and Olive (1953) and summarized with some revisions by Petersen (1974) and Hiratsuka and Sato (1982). Hiratsuka (1973a) discussed the nuclear cycle in relation to the terminology of the spore stages.

This article reexamines previously reviewed studies on the nuclear cycle and associated metabasidium development in microcyclic rust fungi and incorporates those works that were published in the past 20 years and are pertinent to the discussion.

Types of nuclear cycle and accompanying morphological changes in metabasidium and basidiospore production

Type I: Sexual cycle with haploid binucleate mycelium and four haploid uninucleate basidiospores produced on the four-celled metabasidium (Fig. 1)

This type is equivalent to the “variation 1” of Jackson (1935), the “type 1” of Petersen (1974), and the “type I” of Hiratsuka and Sato (1982).

In this nuclear cycle, the vegetative mycelium is at first uninucleate, becoming binucleate during the initiation of a telium (basidiosorus) by various methods described elsewhere. Nuclear fusion takes place in young teliospores

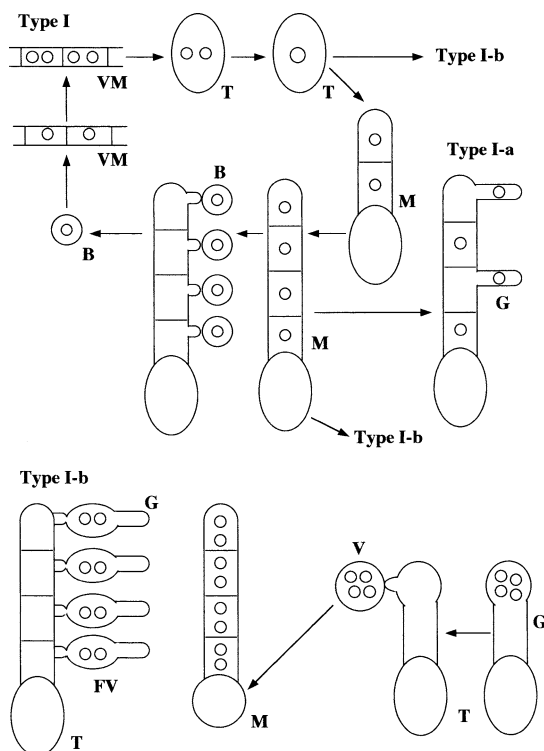


Fig. 1. Types of nuclear cycle in microcyclic rust fungi. *Type I.* A uninnucleate vegetative mycelium (VM) becomes binucleate during telium (basidiosorus) production. Nuclear fusion takes place in a teliospore (T). A fusion (diploid) nucleus divides twice meiotically in a metabasidium (M). Each of four daughter (haploid) nuclei is delimited by septa. Each metabasidium cell produces a uninnucleate basidiospore (B). *Type I-a.* A germ tube (G), instead of an ordinary basidiospore, arises from a metabasidium cell. Two (less frequently one or three) germ tubes are produced from a metabasidium. *Type I-b.* Each metabasidium cell gives rise to a fusiform vesicle (FV), into which a nucleus (presumably haploid) migrates. The nucleus divides mitotically to form two daughter nuclei, which then move to a germ tube (G). In another variant, a nucleus (presumably diploid) in a germ tube (G) from a teliospore divides (presumably meiotically) to form four daughter nuclei. Four daughter nuclei are not delimited by septa; instead, they migrate into a vesicle-like structure (V) formed on an elongated sterigma-like process derived from a germ tube. From the vesicle, another germ tube arises where the four nuclei are delimited by septa and each of four nuclei further divides once mitotically. The germ tube that becomes four celled, each cell containing either one or two nuclei, is referred to as the metabasidium (M). Each binucleate cell may give rise to a germ tube that functions as an infection hypha

(probasidia). During metabasidium production by the germination of teliospores, the fusion (diploid) nucleus divides twice meiotically and each of the four daughter (haploid) nuclei is delimited by septa laid down concomitantly with the nuclear division, the mature metabasidium thus becoming four celled. Each metabasidium cell gives rise to a basidiospore into which the nucleus migrates from the metabasidium cell. In endocyclic species, teliospores may morphologically resemble aeciospores of related macrocyclic species.

This type of nuclear cycle commonly occurs in macrocyclic and demicyclic species but less frequently in microcyclic species. Microcyclic species that exhibit this nuclear cycle type include *Puccinia malvacearum* Bertero (Blackman and

Fraser 1906; Olive 1911; Werth and Ludwigs 1912; Moreau 1914; Lindfors 1924; Allen 1933), *Gymnoconia nitens* (Schwein.) F. Kern & Thurst., pro parte (Kunkel 1914), *Endophyllum sempervivi* (Alb. & Schwein.) de Bary (Maire 1900; Hoffman 1912; Moreau and Moreau 1918b; Ashworth 1935), *E. paederiae* F. Stevens & Mendiola (Ono 2003), *P. prostii* Moug. (Lamb 1934; Olive 1953), *P. grindeliae* Peck (Brown 1940), *P. xanthii* Schwein. (Brown 1940), *P. ruelliae* (Berk. & Broome) Lagerh. (Singh 1979), *P. tiarellaecola* Hiratsuka, f. (Ono 2003), *Cystospora oleae* Butler, pro parte (Thirumalachar 1945), *Kuehneola japonica* (Dietel) Dietel (Kohno et al. 1975b, 1977; Ono 2002), and *Uromyces rayssiae* Y. Anikster & I. Wahl (Anikster et al. 1980).

Puccinia pampeana Speg. was considered to have a demicyclic life cycle with spermogonia, aecia, and telia on *Capsicum* spp. and other solanaceous plants until Hennen et al. (1984) determined its true biology. They found that *Endophyllum*-type and *Puccinia*-type teliospores are produced from the same mycelium after cross-fertilization in spermogonia and that both types of spores germinate to form a four-celled metabasidium with a basidiospore on each metabasidium cell (Hennen et al. 1984). This life cycle is better considered as microcyclic with dimorphic telial states (*Puccinia* and *Endophyllum*) because either one of the telial stages can be deleted for persistence (see also *Puccinia japonica* Dietel; Kakishima et al. 1984).

Haploid uninnucleate basidiospores commonly become binucleate by an additional mitotic division of the nucleus (Anikster 1983, 1984, 1986). Either one of the two or both nuclei migrate into a germ tube. Only one of them seems to take part in the infection, another becoming degenerated. Consequently, a uninnucleate intercellular mycelium results by the infection of an uninnucleate infection hypha. When the basidiospore gives rise to a second basidiospore by "germination by repetition," one of the two nuclei migrates into the secondary basidiospore.

Type I-a: A variation of type I with the production of a uninnucleate germ tube, instead of an ordinary basidiospore, from each uninnucleate metabasidium cell (Fig. 1)

Meiosis takes place in a metabasidium developed from aeciospore-like teliospores, where karyogamy preceded the meiosis. The metabasidium becomes four celled. However, a germ tube, instead of an ordinary basidiospore, arises from the metabasidium cell. Two (less frequently one or three) germ tubes are produced from the metabasidium. This variation has been reported for *Endocronartium harknesii* (J.P. Moore) Y. Hirats. and *E. pini* (Pers.) Y. Hirats. (Hiratsuka 1968, 1969, 1973a, b, 1986; Hiratsuka and Maruyama 1968; Hiratsuka et al. 1966). Contrary to the repeated reports of the above-described nuclear cycle in *Endocronartium* species by Hiratsuka and coworkers, Epstein and Burlage (1988) and Vogler et al. (1997) have shown both cytologically and by an isozyme study that the populations of the fungus named *E. harknesii* reproduce vegetatively. The two nuclei in the aeciospores do not fuse,

and no meiosis takes place in the rust populations they studied. Therefore, they believe that what is named *E. harknessii* must be asexually reproducing and that the fungus name should be *Peridermium harknessii* J.P. Moore.

The same disagreement exists for *E. pini* (Hiratsuka 1969, 1973b) and *Peridermium pini* (Pers.) Lév. (Gibbs et al. 1988). Kasanen (1998) concluded from a molecular analysis that *P. pini* is vegetatively propagated. It has not been determined whether these disagreements are the result of the difference in rust populations they studied or a matter of interpretation of nuclear behavior.

Type I-b: A variation of type I with the production of a binucleate vesicle or a binucleate germ tube, instead of an ordinary basidiospore, from each uninucleate metabasidium cell (Fig. 1)

Gardner (1988) described this variation of nuclear cycle in *Puccinia vittata* J.F. Hennen & Hodges which occurs on *Euphorbia olowaluana* Sherff var. *gracilis* (Rock) Sherff in Hawaii (Hennen and Hodges 1981). A four-celled metabasidium is formed after division (presumably meiosis) of a nucleus (presumably diploid) that has migrated from a teliospore. Each of the four metabasidium cells gives rise to a fusiform vesicle-like structure, into which the nucleus migrates. The nucleus then divides mitotically to form two daughter nuclei. The binucleate vesicle can be referred to as a sedentary basidiospore, and a slender germ tube arising from the vesicle may function as an infection hypha.

A slightly complex, but still basically the same, process of nuclear behavior and associated morphological change in a metabasidium has been reported in *Uromyces alyxiae* Arthur parasitic on *Alyxia olivaeformis* Guad. in Hawaii (Gardner 1987). In a germ tube developing from a teliospore, a nucleus (presumably diploid) divides twice (presumably meiotically) to form four daughter nuclei. The nuclei are not delimited by septa; instead, they migrate into a vesicle-like structure formed on an elongated sterigma-like process derived from the germ tube. From the vesicle, another germ tube arises where the four nuclei are delimited by septa and each of the four nuclei further divides once mitotically. Perhaps, each of the binucleate cells gives rise to a germ tube that functions as an infection hypha although no further observation was made by Gardner (1987). The germ tube that becomes four celled, each cell containing either one or two nuclei, is referable to as a metabasidium and a germ tube possibly developed from each cell is a sedentary basidiospore. This interpretation is contrary to Gardner's view, which considers the tetranucleate vesicle as a basidiospore (Gardner 1987).

Type I-c: A variation of type I with the production of a septate trinucleate or a nonseptate tetranucleate metabasidium (Fig. 2)

This nuclear cycle type has been reported in *Uromyces aloes* (Cook) Magnus on *Aloe* spp. (Thirumalachar 1946; Sato et al. 1980). In this fungus, the vegetative mycelium is at first

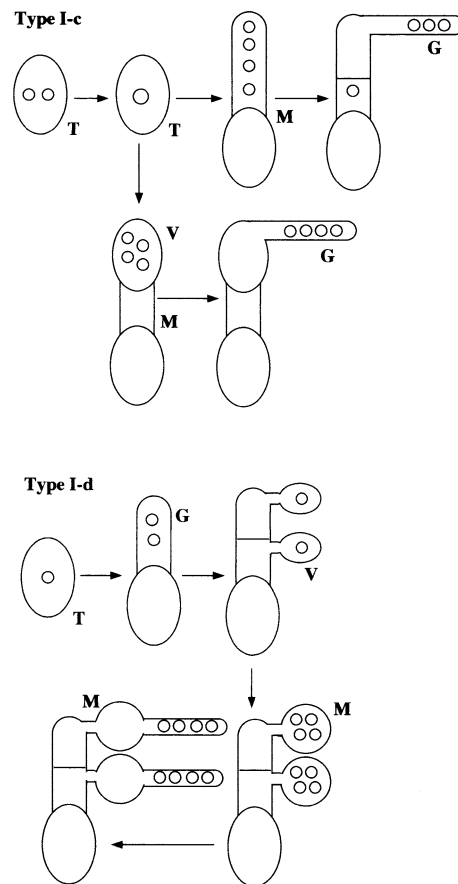


Fig. 2. Types of nuclear cycle in microcyclic rust fungi. *Type I-c.* Distal three haploid nuclei are delimited by a septum from a proximal nucleus in a metabasidium (*M*) or four haploid nuclei locate in an apical vesicle-like structure (*V*) in a metabasidium. The metabasidium or the vesicle gives rise to a thin germ tube (*G*), into which three or four nuclei migrate. *Type I-d.* A uninucleate (presumably diploid) teliospore (*T*) germinates into a germ tube (*G*), where a nucleus divides (presumably mitotically) once to form two daughter nuclei. Two daughter nuclei are delimited by a septum and the germ tube becomes two celled. The apical portion of the germ tube becomes vesicular (*V*). The nucleus migrates into the vesicle. The vesicle becomes a metabasidium (*M*), where the nucleus divides (presumably meiotically) to form four (presumably haploid) daughter nuclei. The four nuclei migrate into a thin germ tube that arises from the vesicle

uninucleate (presumably haploid), and cell fusion is stated to occur between the uninucleate hyphae in a telium. The binucleate mycelium gives rise to binucleate teliospores. The two nuclei then fuse to form a single large (presumably diploid) nucleus. The fusion nucleus undergoes two consecutive divisions (presumably meiosis) to form four daughter nuclei in a metabasidium produced upon the germination of teliospores. A single septum usually divides the metabasidium into a lower uninucleate cell and an upper trinucleate cell. Instead of producing a basidiospore, a whiplike germ tube develops from the upper cell and the three nuclei migrate into it. The germ tube is referable to a nondetachable basidiospore and functions as an infection hypha. Thirumalachar (1946) assumed that uninucleate hyphae are the result of the septation of the trinucleate infec-

tion hypha. In contrast, Sato et al. (1980) speculated that, when intercellular hyphae arise from a trinucleate vesicle formed by the infection of the trinucleate infection hypha, only one nucleus is delimited by a septum. A single teliospore inoculation resulted in telium production with or without spermogonia (Thirumalachar 1946). The spermogonia are apparently nonfunctional. Because of the assumed haploid uninucleate condition in the vegetative mycelium and because of telium production by a single basidiospore inoculation, the homothallic nature of this fungus is proven (Thirumalachar 1946). Olive (1953) stated that this species is basically heterothallic and that the infection hypha is "miktopalontic" homothallic, i.e., secondary homothallic.

This type of nuclear behavior and the associated morphological change of the metabasidium has also been observed in *Endocronartium sahoanum* Imazu & Kakish. var. *sahoanum* (Imazu et al. 1989), *E. sahoanum* var. *hokkaidoense* Imazu & Kakish. (Imazu and Kakishima 1992), and *E. yamabense* (Saho & I. Takah.) Paclt (Imazu et al. 1991a,b). In these fungi, spermogonia are believed to play an important role in the initiation of a binucleate vegetative mycelium. The binucleate mycelium gives rise to binucleate teliospores, which morphologically resemble aeciospores of related *Cronartium ribicola* J.C. Fischer. The two nuclei (presumably haploid) in the teliospores migrate into a metabasidium where the two nuclei fuse to become a single nucleus (presumably diploid). The fusion nucleus then divides (presumably meiotically) twice to form four daughter nuclei in a terminal vesicle-like structure, which is separated from the rest of the metabasidium by a septum. The tetranucleate vesicle gives rise to a thin germ tube, into which the four nuclei migrate. The germ tube is comparable to a sedentary basidiospore and may function as an infection hypha.

In *E. yamabense*, another type (type IX-a) of nuclear cycle was occasionally observed (Imazu et al. 1991a). Hiratsuka (1986) believed that the fungus is uninucleate throughout the life cycle, where no karyogamy and meiosis take place, and that it should be referred to as anamorphic *Peridermium yamabense* Saho & I. Takah. because of the "asexual" nature of reproduction. The population studied by Hiratsuka (1986) might be a haploid variant derived from the population of *E. yamabense* studied by Imazu et al. (1991a).

Endoraecium acaciae Hodges & D.E. Gardner and *E. hawaiiense* Hodges & D.E. Gardner produce teliospores, which morphologically resemble aeciospores and urediniospores of the related species *Atelocauda koae* (Arthur) Cummins & Y. Hirats. on *Acacia koa* Gray var. *koa* in Hawaii (Hodges and Gardner 1984). The nuclear behavior is essentially the same as in *Endocronartium* species. However, in these fungi, one or more short branches arise from the distal vesicular cell. Hodges and Gardner (1984) speculated that the haploid mycelium would result from the infection of one or more of the branches derived from the distal cell and that the binucleate mycelium would be produced by fusion of the uninucleate hyphal cells.

Type I-d: A variation of type I with the production of one or two tetranucleate vesicular metabasidia from a two-celled germ tube derived from teliospores (Fig. 2)

Atelocauda koae (Arthur) Cummins & Y. Hirats. parasitic on *A. koa* var. *koa* in Hawaii exhibits this kind of nuclear behavior and metabasidium production (Gardner 1981; Chen et al. 1996). Uninucleate (presumably diploid) teliospores germinate into a germ tube, into which a nucleus migrates. The nucleus divides (presumably mitotically) once to form two daughter nuclei, and less frequently one of the two nuclei further divides (presumably mitotically). The daughter nuclei are delimited by a septum laid down concomitantly with the nuclear division. Thus, the germ tube is now two celled, or less frequently three celled, and becomes branched. The distal end of the branched germ tube becomes vesicular. The nucleus migrates into the terminal vesicle of the germ tube branch and divides (presumably meiotically) to form four daughter nuclei. The four nuclei then migrate into a thin germ tube that arises from the terminal vesicle.

Gardner (1981) and Chen et al. (1996) interpreted the tetranucleate vesicle as representing a vestigial basidiospore or a nondetachable basidiospore, suggesting the two- or three-celled germ tube from the teliospores to be a metabasidium. Their interpretation of the tetranucleate vesicle as the basidiospore might be derived from a general observation that mature basidiospores of various rust fungi have been often reported to become binucleate or even regularly tetranucleate (Anikster 1983, 1984). The tetranucleate vesicle observed in *A. koae* resembles the tetranucleate basidiospores of a number of *Uromyces* and *Puccinia* species (Anikster 1984). However, the four nuclei in basidiospores of various rust fungi reported by Anikster (1984) are the product of a mitotic division of the two nuclei originally contained in the basidiospores. On the other hand, the four nuclei in the vesicle of *A. koae* are a meiotic tetrad. Therefore, the terminal vesicle in which meiosis takes place is better referred to as a metabasidium and the thin germ tube that arises from the vesicle as a basidiospore without dispersal ability.

Atelocauda koae produces spermogonia and uredinioid aecia in addition to telia. However, aeciospores are found to be nonfunctional, i.e., they do not infect the host even though germinating on the host surface (Chen et al. 1996). Chen et al. (1996) speculated that the tetranucleate infection hypha could create a uninucleate hypha by septation of the infection hypha, whereas Gardner (1981) assumed that single infection of the tetranucleate hypha would result in spermogonia of both mating types.

Puccinia rutainsulara D.E. Gardner occurs on *Melicope anisata* (H. Mann) T. Hartley & B. Stone in Hawaii (Gardner 1994). In this fungus, upon germination, a teliospore nucleus (presumably diploid) migrates into a germ tube where it divides (presumably mitotically) to form two daughter nuclei. The germ tube becomes two celled by a septum laid down between the two nuclei. Infrequently, the germ tube becomes tri- or tetranucleate, but only the distal nucleus in a row of three or four becomes delimited

by a septum. From the distal cell, a vesicle-like structure arises and the nuclei that migrate from the cell divide (presumably meiotically) to form four daughter nuclei. The proximal cell(s) remains unchanged. Gardner (1994) interpreted this to indicate that the tetranuclear vesicle is a nondetachable basidiospore as in *A. koae*. However, as stated earlier, the tetranucleate structure derived from the proximal germ tube cell is a metabasidium.

The nuclear behavior and associated morphological changes taking place during the germination of teliospores in *Puccinia rugispora* D.E. Gardner, which occurs on *Zanthoxylum dipetalum* Mann in Hawaii, is somewhat complicated (Gardner 1996), yet it is basically the same as that which is observed in *A. koae* and *P. rutainsulara*. In this fungus, a germ tube that arises from teliospores is a large bubble-like vesicle, instead of a cylindrical tube as in the latter two species. In the vesicular germ tube, a nucleus (presumably diploid) that has migrated from the teliospores divides (presumably mitotically) to form two daughter nuclei. The two nuclei are separated by a septum, the vesicular germ tube thus becoming two celled. Either only the upper cell or both cells give rise to a small vesicle on a sterigma. The nucleus migrates from the germ tube into the vesicle, where it divides twice (presumably meiotically) to form four daughter nuclei. Again, Gardner (1996) interpreted the tetranucleate vesicle as a basidiospore. However, it is an infection hypha that is comparable to a basidiospore and the vesicle is a metabasidium.

Type II: Sexual cycle with the haploid binucleate mycelium and two haploid binucleate basidiospores produced on the two-celled metabasidium (Fig. 3)

This type is equivalent to the “variation 3” of Jackson (1935), the “type 3” of Petersen (1974), and the “type III” of Hiratsuka and Sato (1982).

The vegetative mycelium is binucleate. Two nuclei fuse in young teliospores. After the first meiotic division of the fusion (diploid) nucleus in a metabasidium developing from the teliospores, a septum is laid down between the two daughter (haploid) nuclei. The mature metabasidium is two celled. In each of the two metabasidium cells, the second meiotic division takes place but no septum is formed following the second division. Each metabasidium cell gives rise to a basidiospore, which receives the two nuclei from the metabasidium cell. The two nuclei in the basidiospore are meiotic diads and, thus, the binucleate condition exhibited in this type must not be confused with the binucleate basidiospores commonly observed in many species (Anikster 1983, 1984), whose nuclei are the result of mitosis. Infection of the binucleate basidiospore is believed to initiate a binucleate vegetative mycelium. The two nuclei in any of the basidiospores may be heterokaryotic or homokaryotic, i.e., heterozygous or homozygous in any given gene locus.

This type has been reported in *Puccinia arenariae* (Schumach.) G. Winter (Lindfors 1924), *P. horiana* Hennings (Kohno et al. 1974, 1975a), *P. anemones-virginiana* Schwein., *P. heucherae* (Schwein.) Dietel

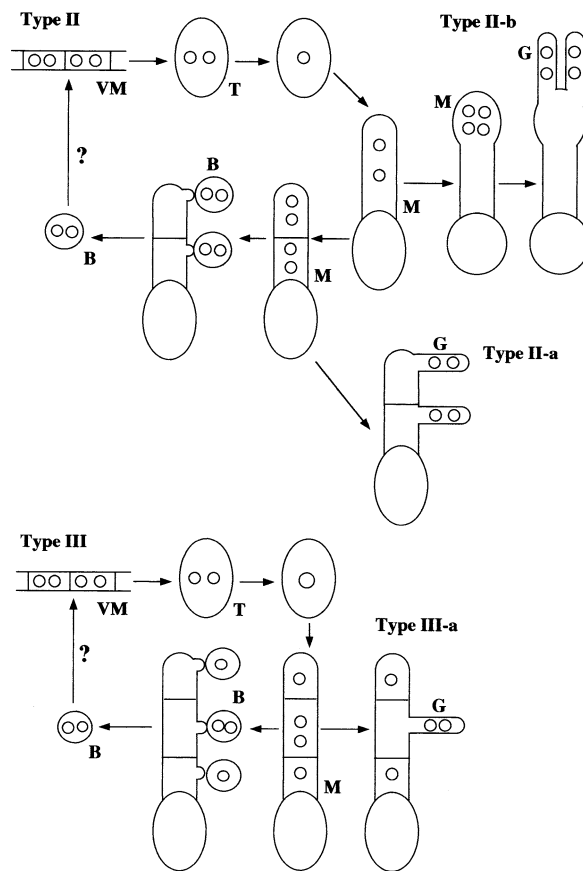


Fig. 3. Types of nuclear cycle in microcyclic rust fungi. *Type II.* A binucleate vegetative mycelium (VM) gives rise to a teliospore (T) where two nuclei fuse. After the first meiotic division of a fusion nucleus, two daughter nuclei are delimited by a septum. In each metabasidium cell (M), the second meiotic division takes place without laying down a septum. Each binucleate metabasidium cell gives rise to a binucleate basidiospore (B). *Type II-a.* A metabasidium cell gives rise to a binucleate germ tube (G), instead of an ordinary basidiospore. *Type II-b.* A nucleus divides once (presumably meiotically) in a metabasidium (M), and two daughter nuclei migrate into a terminal vesicle where the two nuclei undergo second division (presumably meiosis). A pair of the daughter nuclei migrates into bifurcate germ tubes (or infection pegs) (G) arising from the terminal vesicle. *Type III.* A teliospore (T) arises from a binucleate vegetative mycelium (VM). Karyogamy occurs normally in the teliospore, and a fusion (diploid) nucleus migrates into a metabasidium (M). Two successive meiotic divisions and concomitant production of septa usually result in proximal and distal uninucleate cells and one middle binucleate cell. Subsequently, two uninucleate basidiospores (B) and a binucleate basidiospore (B) are produced. *Type III-a.* A middle cell of the metabasidium (M) gives rise to a binucleate germ tube (G) instead of an ordinary basidiospore. A lower uninucleate cell does not germinate, and an upper uninucleate cell may or may not germinate

(Lehmann, cited from Jackson 1935), *Cystopsora oleae* Butler, pro parte (Thirumalachar 1945), *Uromyces oliveirae* Y. Anikster & I. Wahl, nine formae speciales of *U. schillarum* (Grev.) G. Winter (Anikster et al. 1980), and *P. mesnieriana* Thüm. (Anikster and Wahl 1985). Three suspected macrocyclic rusts, *U. christensenii* Y. Anikster & I. Wahl, *U. viennot-bourginii* Y. Anikster & I. Wahl, and *U. hordeastris* Guyot f. sp. *marini* Y. Anikster and f. sp. *bulbosibellevaliae-flexuosae* Y. Anikster, also show this type of

nuclear cycle (Anikster et al. 1980). *Uromyces oliveirae*, nine formae speciales of *U. schillarum*, *P. mesnieriana*, *U. christensenii*, *U. viennot-bourginii*, and *U. hordeastri* f. sp. *bulbosi-bellevaliae-flexuosae* regularly produce tetranucleate basidiospores by additional mitosis of two nuclei in basidiospores (Anikster 1984).

Teliospores of *Chrysomyxa weirii* H.S. Jacks. were found to be unique in being a diaspore and germinating on free water, often after water dispersal (Crane et al. 2000). In this fungus, the vegetative mycelium is mostly uninucleate. At the base of a telium, dikaryotization and subsequent karyogamy occur in the mycelium, from which teliospores are produced. During the development of a metabasidium, nuclear division and concomitant septum formation occur, resulting in the production of a two-celled metabasidium. The nucleus in each metabasidium cell further divides and the two daughter nuclei move into a basidiospore subsequently produced on each metabasidium cell. The two nuclei in the basidiospore were stated to divide once or more, the basidiospore thus becoming tetranucleate or multinucleate. They stated that tetranucleate basidiospore could result either if the first and second divisions are meiosis and the third division is mitosis or if the first division is mitosis and the second and third division are meiosis.

Type II-a: A variation of type II with the production of a germ tube, instead of an ordinary basidiospore, from the metabasidium (Fig. 3)

Teliospores of *Monosporidium machili* (Hennings) T. Sato resemble aeciospores of many *Puccinia* species and germinate into a two-celled metabasidium (Stevens 1932; Hiratsuka and Kaneko 1977). The nucleus (presumably diploid) in the teliospores migrates into a metabasidium, where the nucleus divides once (presumably the first meiotic division). The two daughter nuclei are delimited by a septum and then the second division (presumably the second meiotic division) takes place, resulting in two daughter nuclei in each of the two metabasidium cells. The metabasidium cell gives rise to a germ tube, instead of an ordinary basidiospore, into which the two nuclei migrate (Hiratsuka and Kaneko 1977).

In a *M. machili* population examined by Ono (2003), the vegetative mycelium was exclusively uninucleate. Teliospore initials seemed to arise from the mycelial aggregate, whose cells had already become binucleate. The mode by which the binucleate cell arose was not determined. The teliospores were binucleate and the two nuclei did not seem to fuse, even in the mature teliospores. This observation is contrary to that reported by Hiratsuka and Kaneko (1977), who believed that the two nuclei fuse in immature teliospores because uninucleate spores were frequently observed. The teliospores germinated into the two-celled metabasidium after a nuclear division. The two metabasidium cells became binucleate and gave rise to a binucleate whiplike germ tube, instead of producing ordinary basidiospores. Rarely, no septum was laid down between the two nuclei in the metabasidium.

If karyogamy takes place in the teliospores, then the nuclear divisions in the teliospores and metabasidium are meiosis; thus, the nuclear cycle is type II-a. However, if karyogamy does not occur in the teliospores, the nuclear division in the metabasidium is mitosis; thus, the nuclear cycle is type VII-b. The two types of nuclear cycle may represent the existence of two distinct populations in this morphologically circumscribed species, although a possibility that two variations of nuclear cycle may occur in a single population is not ruled out.

Puccinia japonica Dietel was believed to be demicyclic with aecia and telia in the life cycle. According to Kakishima et al. (1984), however, the spores previously referred to as aeciospores are functionally teliospores (endophylloid teliospores). The endophylloid teliospores are initially binucleate but the two nuclei (presumably haploid) fuse in the spores. Nuclear division (presumably meiosis) takes place in a metabasidium produced upon the germination of teliospores. The two-celled, binucleate metabasidium results and a binucleate hypha emerges from each metabasidium cell. Ordinary puccinioid teliospores also germinate into a metabasidium. The nuclear behavior in the metabasidium and basidiospores developing from the puccinioid teliospores follows the pattern of type III-a. Similar to *P. pompeana*, the life cycle of this fungus is considered to be microcyclic with dimorphic telial states, i.e., *Puccinia* and *Endophyllum*.

Type II-b: A variation of type II with the development of bifurcate infection hyphae, instead of an ordinary basidiospore, from the metabasidium (Fig. 3)

Although the nuclear cycle observed in most populations of *Hemileia vastatrix* Berk. & Broome is type I (Chinnappa and Sreenivasan 1965, 1968; Coutinho et al. 1995), a population studied by Rajendren (1967a–c) exhibits a unique nuclear behavior in teliospores that resemble urediniospores, i.e., the uredinioid teliospores. The nuclear cycle is called the “Kamat phenomenon” (Rajendren 1967a–c).

In the population studied by Rajendren (1967a,b), the binucleate vegetative mycelium became uninucleate, presumably by karyogamy, then produced sporogenous (basidiogenous) cells. Uredinioid spores were produced from the uninucleate (presumably diploid) mycelium. Upon the germination of spores, the nucleus divided once (presumably first meiotic division) and the two daughter nuclei migrated into a terminal vesicle of a germ tube. The two nuclei then underwent a second division (presumably second meiotic division). A pair of the four daughter nuclei migrated into each of the bifurcate infection pegs arising from the terminal vesicle. This process often repeated once or twice so that secondary or tertiary vesicles were produced. The binucleate uredinioid spores were considered as functional teliospores because the two nuclei in the spores were interpreted as transient meiotic diads. The terminal vesicle was comparable to a metabasidium.

In addition to the aforementioned “atypical, nonsporidial” germination in the uredinioid teliospore, “the typi-

cal, sporidial" germination was reported in the same population (Rajendren 1967c). The spores gave rise to a two- to four-celled metabasidium, from which a maximum of two basidiospores were produced. No nuclear condition for this process was reported, however. Hennen and Figueiredo (1984) believed that the spores functioning as teliospores in *H. vastatrix* are derived from aeciospores, rather than urediniospores as Rajendren (1967a–c) stated, because the life cycle reduction normally occurs either in the "telioid" pathway or in the "endophylloid pathway" (Hennen and Buritica 1980) and because the *Hemileia* population that exhibits the Kamat phenomenon is most likely to be derived through the endophylloid pathway. In the so-called endophylloid pathway, the aeciospores of the parental macrocyclic species become the functional teliospores whereas the morphology remains unchanged. However, a spermogonial aecial stage has not been found in any *Hemileia* species.

Type III: Sexual cycle with the haploid binucleate mycelium and one haploid binucleate and two haploid uninucleate basidiospores produced on the three-celled metabasidium (Fig. 3)

This type is equivalent to the "type 7" of Petersen (1974) and the "type IV" of Hiratsuka and Sato (1982). No equivalent "variation" is found in Jackson (1935).

The vegetative mycelium is binucleate. Teliospores arise from the binucleate mycelium. Karyogamy occurs normally in the teliospores, and the fusion (diploid) nucleus migrates into a metabasidium developing by the germination of teliospores. Two successive meiotic divisions take place, resulting in four haploid nuclei. Instead of laying down three septa to delimit the four daughter nuclei, however, only two septa are laid down, usually forming two proximal and distal uninucleate cells and one middle binucleate cell. Subsequently, three basidiospores are produced, i.e., two uninucleate basidiospores from the proximal and distal metabasidium cells and a binucleate basidiospore from the middle metabasidium cell. Again, the two nuclei in the basidiospore are meiotic diads, and thus the binucleate condition exhibited in the type must not be confused with binucleate basidiospores commonly observed in many other species (Anikster 1983, 1984), in which mitosis results in the binucleate condition. Infection of the binucleate basidiospore is believed to initiate the binucleate mycelium.

This type has not been known in microcyclic rust species but is reported for a macrocyclic (or brachycyclic) species, *Sphenospora kevorkianii* Linder (Olive 1947), and two demicyclic species, *Gymnosporangium clavipes* (Cooke & Peck) Cooke & Peck (Olive 1949) and *Uromyces erythronii* (DC.) Pass. (Fukuda and Nakamura 1990). In *S. kevorkianii*, the middle metabasidium cell is binucleate and the apical and basal cells are uninucleate. Occasionally, two- and four-celled metabasidia are produced (Olive 1947). This type of nuclear behavior was rarely observed in *G. clavipes* (Olive 1949).

Fukuda and Nakamura (1990) reported that populations of *U. erythronii* on *Erythronium japonicum* Decne. and *Amana edulis* (Miq.) Honda produced three-celled metabasidia whereas a population on *A. latifolia* (Makino) Honda formed four-celled metabasidia. In the former populations, the middle cell of the metabasidium was binucleate whereas the apical and basal cells were uninucleate. They attributed the frequent lack of spermogonia in the aecial stage in the former populations to the consistent production of binucleate basidiospores, indicating the origin of a binucleate vegetative mycelium by the infection of binucleate basidiospores. In the latter population, which consistently produced four uninucleate basidiospores, however, aecia were always associated with spermogonia in the natural infection.

Whether the two nuclei of the binucleate basidiospores are heterozygous for any given gene would depend on two factors: (1) which two of the four daughter nuclei are included in the binucleate metabasidium cell and (2) the segregation pattern of the genes involved (Petersen 1974). If *S. kevorkianii* and *U. erythronii* should prove to be heterothallic, then it would appear that the binucleate basidial cells and the basidiospores produced by them are "miktohaplontic" homothallic (Buller 1941; Olive 1953) or secondary homothallic.

Type III-a: A variation of type III with the production of a germ tube, instead of an ordinary basidiospore, from the metabasidium (Fig. 3)

This mode of nuclear cycle has been known only in *P. japonica*. As described in nuclear cycle type II-a, this fungus produces two (puccinioid and endophylloid) types of teliospores in the life cycle. The puccinioid teliospores form a three-celled metabasidium upon germination, with the middle cell being binucleate. The middle cell gives rise to a germ tube, into which two nuclei (presumably haploid) migrate. The lower uninucleate cell does not germinate, and the upper uninucleate cell may or may not germinate. This species possesses the endophylloid teliospores whose nuclear cycle is of type II-a, as described earlier. It is interesting to note that, when the puccinioid teliospores are inoculated, the production of the endophylloid telium precedes the puccinioid telium, whereas both endophylloid and puccinioid telium arise simultaneously when the endophylloid teliospores are inoculated (Kakishima et al. 1984).

Type IV: Sexual cycle with the haploid binucleate or uninucleate mycelium and two haploid uninucleate basidiospores produced on the two-celled metabasidium (Fig. 4)

This type of nuclear behavior and metabasidium formation was found for the first time in *Herpobasidium filicinum* (Rostr.) Linder (Platyglouaceae, Platyglouales) (Jackson 1935). In *H. filicinum*, the vegetative mycelium both in and on the surface of the host plant is binucleate. The two nuclei

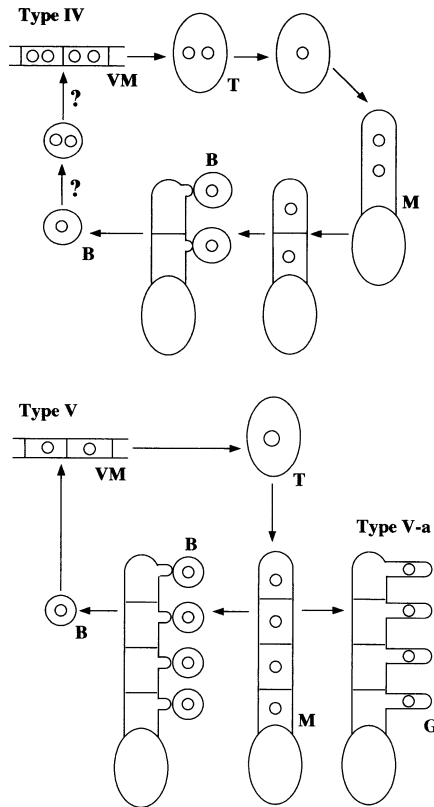


Fig. 4. Types of nuclear cycle in microcyclic rust fungi. *Type IV.* A binucleate teliospore (*T*) arises from a binucleate vegetative mycelium (*VM*). Karyogamy takes place in the teliospore, and a fusion (diploid) nucleus divides once (presumably first meiosis) and septum formation follows in the metabasidium (*M*). Each metabasidium cell gives rise to a uninucleate basidiospore. *Type V.* A teliospore (*T*) arises from a uninucleate (presumably diploid) vegetative mycelium (*VM*). A nucleus divides twice (presumably mitotically) in a metabasidium (*M*). The four (presumably diploid) nuclei are delimited by septa laid down between the nuclei. Each metabasidium cell gives rise to a uninucleate basidiospore. *Type V-a.* A whiplike germ tube (*G*), instead of an ordinary basidiospore, arises from each metabasidium cell (*M*)

fuse in a distal cell of the branched mycelium. The distal cell containing a fusion nucleus (presumably diploid) then becomes a metabasidium. The fusion nucleus divides once (presumably first meiosis) and the daughter nuclei (presumably haploid) are separated by a septum laid down between them. Each of the two metabasidium cells gives rise to a sterigma on which a basidiospore is formed. The nucleus in the metabasidium cell migrates into the basidiospore. A mode of dikaryotization was unknown to Jackson (1935), but he assumed that a second meiosis took place in the basidiospore, suggesting the origin of the binucleate vegetative mycelium by infection of the binucleate basidiospore. If this is true, then *H. filicinum* is considered to be homothallic.

In the rust fungi, this nuclear cycle type was found to occur in *Puccinia circaeae* Pers. (Ono 2003). The vegetative mycelium was mostly uninucleate, and the binucleate condition was rarely observed. Dikaryotization seemed to occur in a telium primordium, although the mode of dikaryotization was not determined. Teliospores were

initially binucleate but became uninucleate through karyogamy in the course of the maturation. The teliospores germinated into a two-celled metabasidium. Each of the two metabasidium cells contained one nucleus and formed a uninucleate basidiospore. The nuclear division that takes place in the metabasidium development is believed to be the first meiotic division. The nucleus in the basidiospore then divided once more to form two daughter nuclei. This additional division can be interpreted as the second meiotic division. Very often, two nuclei migrated into a germ tube upon the germination of basidiospores. Although this has not been observed, the infection of the binucleate basidiospore is believed to initiate the uninucleate vegetative mycelium with an unidentified mode. Thus, this fungus is homothallic in the sexual reproduction.

Type V: Apomictic cycle with the entirely diploid uninucleate mycelium and four diploid uninucleate basidiospores produced on the four-celled metabasidium (Fig. 4)

This type is equivalent to the “variation 6” of Jackson (1935), the “type 6” of Petersen (1974), and the “type VIII” of Hiratsuka and Sato (1982).

In this type of nuclear cycle, the vegetative mycelium is believed to be diploid uninucleate. Teliospores arise from the uninucleate mycelium. The nucleus of teliospores passes into a metabasidium developing through the germination of teliospores and divides twice (presumably mitotically). The four nuclei (presumably diploid) are delimited by septa laid down between the nuclei. Thus, the mature metabasidium becomes four celled. Each of the four metabasidium cells gives rise to a sterigma on which a basidiospore is formed. The basidiospore receives the single nucleus from the metabasidium cell. Thus, the nuclear cycle is wholly diploid.

This type of nuclear behavior and metabasidium formation have been reported for a large uninucleate form of *Endophyllum euphorbiae-sylvaticae* (DC.) G. Winter (= *E. euphorbiae* Plowr., *E. uninucleatum* Moreau) (Moreau 1911, 1914, 1915; Moreau and Moreau 1918a, 1919; Dodge 1929; Olive 1953). This type has also been observed in a form of demicyclic *Puccinia podophylli* Schwein. (Brumfield, cited from Dodge 1929).

Dodge (1929) considered that the nucleus observed in the vegetative mycelium and the teliospores of the large uninucleate form of *E. euphorbiae-sylvaticae* is diploid, because the spores of the uninucleate form are as large as those of the binucleate form, and that the four-celled metabasidium is produced by nuclear divisions without actual reduction. In contrast to Dodge (1929), Petersen (1974) interpreted the nuclear division during metabasidium development in *E. euphorbiae-sylvaticae* as meiosis, and Hiratsuka and Sato (1982) apparently followed him without referring to Dodge’s (1929) interpretation. Dodge (1929) assumed that *E. uninucleatum* and the uninucleate form of *E. euphorbiae-sylvaticae* have evolved from the parental form by fusion of two haploid nuclei in the vegetative mycelium, which does not normally occur in the parental form.

A uninucleate form of *Aecidium punctatum* Pers. and of *A. leucospermum* DC. reported by Kursanov (1917) may be interpreted as an endocyclic derivative of *Tranzschelia pruni-spinosae* (Pers.) Dietel and *Ochropsora ariae* (Fuckel) Ramsb., respectively. The nucleus is assumed to be diploid; thus, the nuclear cycle of these fungi is expected to follow this type. However, Dodge (1929) predicted that the uninucleate aeciospores would result in uninucleate teliospores upon infection on the alternate host.

The nuclear cycle of *Puccinia lantanae* Farl. (Ono 2002) is temporarily classified as this type, although the ploidy of the nucleus observed is not determined. If the nucleus is proven to be haploid, the nuclear cycle would be a new variation of type VI.

Type V-a: A variation of type V with the production of a whiplike germ tube, instead of an ordinary basidiospore, from the metabasidium (Fig. 4)

This variation of nuclear cycle is reported only in *Puccinia patriniae* Hennings (Ono 2002). The nuclear cycle of this fungus is the same as that of *P. lantanae*; however, a whip-like germ tube, instead of an ordinary basidiospore, arises from each metabasidium cell (Ono 2002). As in *P. lantanae*, the ploidy of the nucleus observed throughout the nuclear cycle is not determined; thus, the placement is arbitrary.

Type VI: Apomictic cycle with the haploid binucleate mycelium and four haploid uninucleate basidiospores produced on the four-celled metabasidium (Fig. 5)

This type is equivalent to the “variation 2” of Jackson (1935), the “type 2” of Petersen (1974), and the “type II” of Hiratsuka and Sato (1982).

The vegetative mycelium is binucleate. Teliospores arise from the binucleate mycelium. No nuclear fusion takes place, and the two haploid nuclei migrate into a metabasidium produced by the germination of teliospores. The two nuclei subsequently divide (presumably mitotically) to form four daughter nuclei, which are concomitantly separated by septa. Each of the four metabasidium cells gives rise to a basidiospore that receives a single nucleus. Although the pattern is similar to type I, karyogamy and subsequent meiosis do not occur. Thus, the nuclear cycle is entirely haploid.

This mode of nuclear cycle has been observed so far only in a binucleate form of *Gymnoconia nitens* (Kunkel 1914; Dodge and Gaiser 1926; Dodge 1929; Olive 1953) and a binucleate form of *E. euphorbiae-sylvaticae* (Sappin-Trouffy 1896; Moreau 1911, 1914, 1915; Moreau and Moreau 1918a, 1919; Dodge 1929; Olive 1953).

Type VII: Apomictic cycle with the production of two haploid binucleate basidiospores produced on the two-celled metabasidium (Fig. 5)

This type was first recognized as distinct and designated as type V by Hiratsuka and Sato (1982).

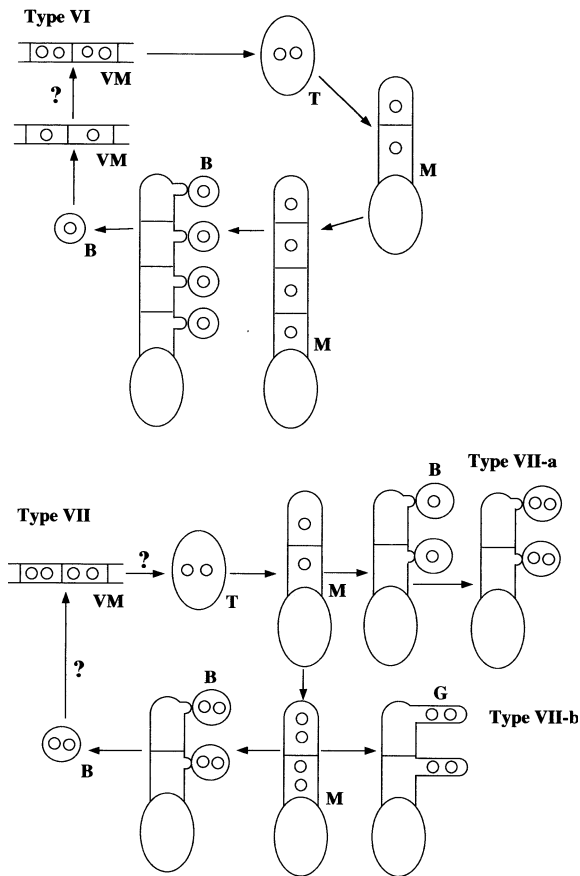


Fig. 5. Types of nuclear cycle in microcyclic rust fungi. *Type VI.* A teliospore (*T*) arises from a binucleate vegetative mycelium (*VM*). No nuclear fusion takes place, and two haploid nuclei migrate into a metabasidium, where they divide (presumably mitotically) to form four daughter nuclei. Each metabasidium cell gives rise to a uninucleate basidiospore. *Type VII.* A teliospore is binucleate. No nuclear fusion takes place in the binucleate teliospore, and two nuclei divide (presumably mitotically) once in a metabasidium (*M*). Each binucleate metabasidium cell gives rise to a binucleate basidiospore. *Type VII-a.* A binucleate teliospore (*T*) arises from a binucleate vegetative mycelium (*VM*). Two nuclei (presumably haploid) migrate into a metabasidium (*M*). The nuclei are separated by a septum, and each nucleus moves into a basidiospore (*B*). The nucleus in each basidiospore further divides (presumably mitotically). *Type VII-b.* Instead of producing an ordinary basidiospore, a binucleate germ tube (*G*) arises from each metabasidium cell (*M*).

Only *Endophyllum spilanthes* Thirum. & Govindu exhibits this type of the nuclear behavior associated with the metabasidium and basidiospore production (Thirumalachar and Govindu 1954). Teliospores are binucleate, perhaps being derived from a binucleate mycelium. No nuclear fusion takes place in the binucleate teliospores, and the two nuclei divide (presumably mitotically) once in a metabasidium. Each of the two metabasidium cells, which are binucleate, gives rise to a binucleate basidiospore. Upon infection, the binucleate basidiospore is assumed to initiate the binucleate condition of the vegetative mycelium.

Type VII-a: A variation of type VII with the delay of nuclear division in the basidiospores (Fig. 5)

This method has been known only in *Endophyllum heliotropii* Thirum. & Naras. (Thirumalachar and Narasimhan 1950). Teliospores are initially binucleate, and each of the two nuclei migrates into a developing metabasidium upon the germination of teliospores. The nuclei are separated by a septum, and each nucleus moves into a basidiospore subsequently developed on the metabasidium. The nucleus (presumably haploid) in the basidiospore then divides (presumably mitotically). Infection of the binucleate basidiospore is assumed to initiate the binucleate vegetative mycelium.

Type VII-b: A variation of type VII with the production of a binucleate germ tube, instead of an ordinary basidiospore, from the metabasidium cell (Fig. 5)

This nuclear cycle has been known only in one of three endocyclic forms of *Uromyces hobsoni* Vize on *Jasminum grandiflorum* L. (Payak 1953). Teliospores arise from a binucleate vegetative mycelium. A two-celled uninucleate metabasidium is produced upon the germination of teliospores, where karyogamy and subsequent meiosis do not occur. The nucleus (presumably haploid) in each of the two-celled metabasidium divides (presumably mitotically). Each metabasidium cell gives rise to a binucleate germ tube instead of producing an ordinary basidiospore.

Type VIII: Apomictic cycle with the haploid binucleate mycelium and one haploid uninucleate basidiospore produced on the two-celled metabasidium (Fig. 6)

This type is equivalent to the “variation 4” of Jackson (1935), the “type 4” of Petersen (1974), and the “type VI” of Hiratsuka and Sato (1982).

This nuclear cycle has been observed only in *Endophyllum valerianae-tuberosae* R. Maire (Maire 1900; Poirault 1915; Jackson 1931, 1935). The vegetative mycelium is at first uninucleate and becomes binucleate by an unknown mode of dikaryotization. Teliospores are binucleate, and no nuclear fusion takes place in the teliospores. One of the two nuclei degenerates, and the remaining nucleus (presumably haploid) migrates into a metabasidium developing upon the germination of teliospores. The nucleus undergoes another division (presumably mitosis), and a septum divides the metabasidium into two cells. The nucleus in the lower cell degenerates. The upper cell gives rise to a sterigma on which a basidiospore is formed. The basidiospore receives a nucleus from the metabasidium cell.

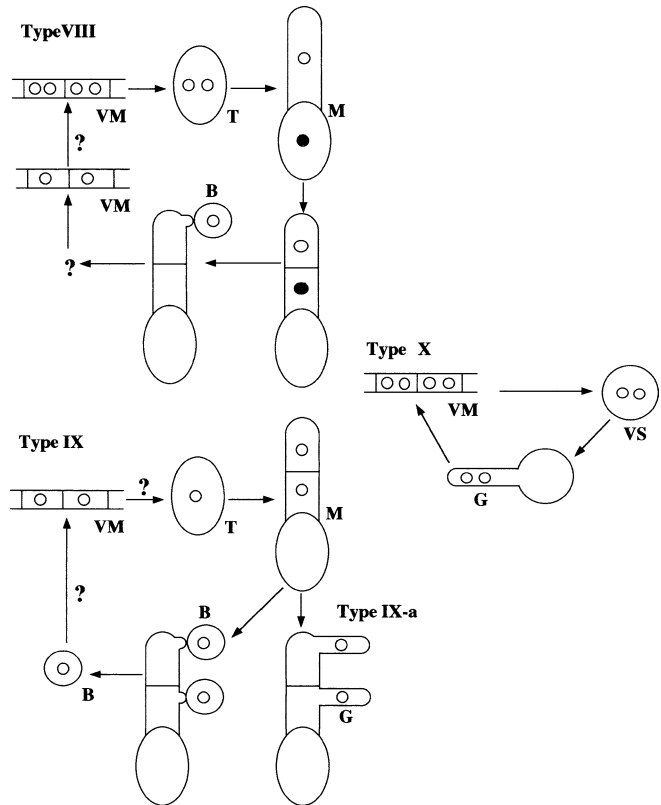


Fig. 6. Types of nuclear cycle in microcyclic rust fungi. *Type VIII.* A vegetative mycelium (VM) is uninucleate. A binucleate teliospore (T) arises from a vegetative mycelium that dikaryotizes through an unidentified method. One of the two nuclei (solid circle) degenerates, and the remaining nucleus (presumably haploid) migrates into a metabasidium. The nucleus undergoes a single division (presumably mitotic), and a septum divides the metabasidium into two cells. The nucleus (solid circle) in the lower cell degenerates. The upper cell gives rise to a uninucleate basidiospore. *Type IX.* A vegetative mycelium (VM) and a teliospore (T) are haploid uninucleate. In a metabasidium (M), a single nucleus (presumably haploid) divides once (presumably mitotically), and a septum is laid down between the daughter nuclei. The mature metabasidium is two celled and each cell gives rise to a uninucleate basidiospore (B). *Type IX-a.* Either an upper cell or both cells of a metabasidium produce a germ tube (infection hypha) (G), instead of an ordinary basidiospore. *Type X.* A vegetative mycelium (VM) is binucleate. No karyogamy and meiosis take place in the production of vegetative spores (VS). The binucleate spore germinates into a binucleate germ tube (G). The process is wholly asexual

Type IX: Apomictic cycle with the haploid uninucleate mycelium and two haploid uninucleate basidiospores produced on the two-celled metabasidium (Fig. 6)

This type is equivalent to the “variation 5” of Jackson (1935), the “type 5” of Petersen (1974), and the “type VII” of Hiratsuka and Sato (1982).

The vegetative mycelium and young teliospores are haploid uninucleate. In a metabasidium developed by the germination of teliospores, the single nucleus (presumably haploid) divides (presumably mitotically) once and a septum is laid down between the daughter nuclei. The mature metabasidium is two celled, and each of the two cells gives rise to a sterigma on which a basidiospore is formed. The

basidiospore receives a single nucleus from the metabasidium cell. Thus, the nuclear cycle is entirely haploid uninucleate.

This type of nuclear behavior has been reported for a small uninucleate form of *G. nitens* (Dodge 1924, 1929; Jackson 1935; Olive 1953), *Uromyces rudbeckiae* Dietel & Holw. (Olive 1911; Jackson 1931), *Endophyllum centranthirubri* G. Poirault (Poirault 1913, 1915; Jackson 1935), and one of three endocyclic forms of *U. hobsoni* (Payak 1953).

Dodge (1929) considers that the single nucleus in the teliospores of a small uninucleate form of *G. nitens* is haploid by contrasting the small-sized teliospores of this form to the large-spored form of *G. nitens*. The nucleus size of the small-spored form is stated to be the same as each of the two nuclei in the large-spored form.

In an endocyclic form of *U. hobsoni* (Payak 1953), the vegetative mycelium, teliospores, and two-celled metabasidium are uninucleate. A binucleate basidiospore seems to arise from each of the two uninucleate (presumably haploid) metabasidium cells after division (presumably mitosis) of the nucleus. Because the vegetative mycelium is uninucleate, one of the two nuclei in the basidiospore is assumed to degenerate during the infection process.

Type IX-a: A variation of type IX with the production of a germ tube, instead of an ordinary basidiospore, from the two-celled metabasidium (see Fig. 6)

A two-celled uninucleate (presumably haploid) metabasidium is produced from uninucleate teliospores. Either an upper cell or both cells of the metabasidium produce a germ tube or an infection hypha, instead of producing an ordinary basidiospore. Populations of the *P. yamabense*-*E. yamabense* complex exhibit this type of nuclear cycle. Hiratsuka (1986) considered that the life cycle of *P. yamabense* he examined is wholly vegetative, however. Imazu et al. (1991a,b) only occasionally observed this nuclear behavior in their material of *E. yamabense*. As mentioned elsewhere, the population referred to as *P. yamabense* (Hiratsuka 1986) may well be a haploid variant derived from the *E. yamabense* population that is truly endocyclic in the life cycle (Imazu et al. 1991a,b).

One of three endocyclic forms of *U. hobsoni* on *Jasminum malabaricum* has also been known to form two uninucleate whiplike germ tubes from the two-celled metabasidium, and the nucleus has been assumed to be haploid (Payak 1953).

Type X: Asexual life cycle with the haploid binucleate vegetative mycelium and spores without the production of metabasidium (see Fig. 6)

The vegetative mycelium is binucleate. Karyogamy and subsequent meiosis do not take place in the production of spores and their germination. Regular conjugate division of the two nuclei and following septation result in spores that are morphologically aeciospores. The process is wholly

asexual. *Aecidium mori* Barclay (Kaneko 1973), *A. raphiolepidis* Syd., and *A. pourthiaee* P. Syd. & Syd. (Sato and Sato 1981) exhibit this type of life cycle.

From long-term field observations, inoculation experiments, and cytological observations, it is apparent that these anamorphic fungi only produce morphological aeciospores in the peridiate *Aecidium*-type sori. The spores and sori of three *Aecidium* species are referred to as the aecidioid urediniospores and aecidioid uredinia, respectively (Kaneko 1973; Sato and Sato 1981). These observations suggest that many unconnected *Aecidium*, *Peridermium*, *Roestelia*, and *Caecoma* species reproduce entirely by the haploid binucleate vegetative spore without a sexual stage in the life cycle. Similarly, many unconnected *Uredo* species are believed to have lost the sexual recombination process.

Loss of sexual recombination process is associated with reduction of life cycle in the rust fungi

The mode of dikaryotization

Sexuality in rust fungi has been a vexing question ever since the suggestion made by Meyen (1841, cited from Blackman 1904) that spermogonia and aecia represent the male and female organ, respectively. This view was first supported by the observations of Tulasne (1854, cited from Blackman 1904) and De Bary (1853, 1884, cited from Blackman 1904), who showed that spermogonia and aecia were closely associated in a large number of species and that spermatia produced in spermogonia apparently lacked ability of germination (cited from Blackman 1904). Since Blackman (1904) first discovered the dikaryotization (fertilization) of the haploid mycelium by nuclear migration, a variety of methods of dikaryotization have been documented with the monumental work on the function of the spermogonium by Craigie (1927a,b). Although the sexual process seems to occur uniformly in macrocyclic rust fungi with the spermogonial-aecial stage, diverse modes of sexual reproduction have been documented or suggested for microcyclic fungi (Walker 1928; Jackson 1931; Petersen 1974).

Jackson (1931) classified microcyclic rust fungi into two categories according to the nuclear status of the vegetative mycelium and suggested two modes of dikaryotization: (1) species with a uninucleate vegetative mycelium, with the binucleate mycelium being initiated by cell fusion or other undetermined methods in the sorus primordium (22 species in *Puccinia*, *Uromyces*, *Tranzschelia*, *Kunkelia* (= *Gymnoconia*), *Gallowaya* (= *Coleosporium*), *Chrysomyxa*, and *Endophyllum*); and (2) species predominantly with a binucleate vegetative mycelium that is initiated by unidentified mode(s) at an early stage of infection (21 species in *Puccinia*, *Uromyces*, and *Botryorhiza*). *Uromyces ficariae* and *P. xanthii* were included in both categories.

The methods of dikaryotization so far reported in microcyclic rust fungi are summarized as follows.

1. Nuclear migration in the telium primordium

Blackman (1904) documented the origin of the binucleate condition by nuclear migration in *Phragmidium violaceum* (Schultz) G. Winter. He first confirmed the nuclear cycle illustrated by Sappin-Trouffy (1896) for the Uredinales. In *P. violaceum*, mature uninucleate teliospores gave rise to four uninucleate basidiospores. A mycelium derived from the basidiospore infection was uninucleate and formed spermatia in spermogonia. Young aecia became binucleate, and the binucleate condition persisted throughout the life cycle until the nuclei fused in mature teliospores. Blackman (1904) interpreted the spermatium as a male cell and the aecium as a female reproductive organ. However, he considered the spermatium that formerly took part in fertilization no longer retained its sexual ability in *P. violaceum* and confirmed that a vegetative mycelial cell was fertilized by a nucleus from an adjacent cell. This process was called a “reduced form of fertilization” by Blackman (1904).

Werth and Ludwigs (1912) found in *Puccinia malvacearum* that cell fusion occurred between uninucleate cells of unequal size and that the nucleus of the smaller migrated to the larger cell (Walker 1928). Lindfors (1924) showed that cell fusion occurred in *Tranzschelia fusca* (Pers.) Diet., although nuclear migration occurred through a small pore if the cells were in contact with each other (Walker 1928). Walker (1928) assumed that the binucleate condition in *U. ficariae* originated, as in *P. malvacearum*, by nuclear migration between cells at the base of a telial primordium, although a possibility of dikaryotization by cell fusion was not ruled out. A similar process was observed in *U. hobsoni* (Payak 1952). In *P. prostii*, the dikaryotic condition was stated to arise at the base of a telial primordium, either by nuclear migration or by cell fusion (Lamb 1934; Olive 1953).

2. Cell fusion in the telium primordium

This second mode of dikaryotization was documented by Christman (1905) for *Gymnoconia nitens* and *Phragmidium speciosum* (Fr.) Cooke. In these rust fungi, uninucleate cells in a telium primordium became aligned in a pair. Each pair of cells came in contact where the wall of the two cells dissolved and the protoplasts were brought into contact. By gradual enlargement of the dissolved area of the walls, the upper halves of the protoplasts of the gametes united to form a continuous cell mass, which still showed the two distinct bases. In all cases, “the two distinct bases remain throughout as an evidence of the double origin of each row of aecidiospores” (Christman 1905). Christman (1905) considered the fused cells observed in *P. speciosum* and *G. nitens* are equal gametes. Christman (1905) also stated that the important problem relating this discovery was that the function of the spermogonium and the spermatium remained unexplained in the life cycle of rust fungi. Craigie (1927a,b) eventually answered this question by sophisticated experiments.

Following Christman’s discovery, Olive (1908a) found that the binucleate condition in *Puccinia transformans* Ellis

& Everh. [= *Prosopodium transformans* (Ellis & Everh.) Cummins] was brought about by the absorption of the walls of two adjacent cells, which came in contact in a telium (Walker 1928). However, Olive (1908b) pointed out that the seeming disagreement between the “Blackman-type” and “Christman-type” of dikaryotization methods may be a matter of degree by which the wall of two adjacent gametic cells are dissolved; in the cytological study of *Triphragmium ulmariae* (Schlect.) Lagerh. and three other rust fungi, he observed Blackman-type dikaryotization through a narrow pore and Christman-type through a broad pore side by side in the same fungal mycelium.

Consequently, intermediate conditions have been observed between the migration of the nucleus from a smaller to a larger cell and the fusion of equal-sized cells. *Puccinia prostii* Moug. was reported to dikaryotize at the base of a telial primordium either by means of cell fusion or by nuclear migration (Lamb 1934; Olive 1953). Lindfors (1924) showed that cell fusion occurred in *T. fusca*, while Walker (1928) stated that dikaryotization took place by nuclear division not followed by septum formation, although cell fusion was occasionally observed.

Dodge (1929) stated that cell fusion is known to occur in more than 40 species. Characteristic cell fusion has been reported in *Gallowaya pinicola* Arth. (= *Coleosporium pinicola* (Arthur) Arthur) (Dodge 1925; Walker 1928), *Puccinia morthieri* Körn. (Lindfors 1924), *P. eatoniae* Arthur (Fromme 1914), *P. thwaitesii* Berk. (= *P. lantanae*) (Payak 1952), *P. xanthii*, *U. ficariae*, and *Chrysomyxa abietis* (Wallr.) G. Winter (Walker 1928), *Endophyllum sempervivi* (Hoffman 1912), and *Uromykladium tepperianum* (Sacc.) McAlpine (Olive 1953).

3. Anastomosis of vegetative mycelia at an early stage of basidiospore infection

Kursanov (1917) noted the migration of a nucleus into a fertile cell from a purely vegetative mycelium in *Uromyces alchemillae* (Pers.) Fuckel (= *Trachyspora alchemillae* Fuckel). Lindfors (1924) showed that cell fusion occurred, at an early stage of infection, between cells of young telia in *P. malvacearum* and that the binucleate cells were often separated by sterile cells. Similarly, dikaryotization in *P. adoxae* and *U. scillarum* seemed to take place by cell fusion of a vegetative mycelium at an early stage of infection (Walker 1928).

Dodge (1929) distinguished the “anastomosis” from the “migration” and the “fusion” as the mode of dikaryotization in rust fungi, whereas Lindfors (1924) stated that the three methods were observed with practically all intergrades in dikaryotization in *T. alchemillae*. In the observed cell fusions, fusing (gametic) cells are stated to be more or less differentiated (Dodge 1929); however, the distinction of the fusing cells from the vegetative cells in a telium primordium is arbitrary. Furthermore, as variously stated here, the difference between migration and fusion is a matter of degree by which the wall of adjacent two cells is dissolved.

4. Mitotic division of a nucleus not accompanied by cell division

The origin of binucleate condition by mitosis not followed by septum formation in a uninucleate mycelial cell was first suggested by Sappin-Trouffy (1896). Walker (1928) interpreted for *Puccinia asteris* Duby, *P. cryptotaeniae* Peck, and *T. fusca* that a binucleate mycelium originated from a uninucleate mycelium by nuclear division not associated with septum formation. Ono (2002) believed that this phenomenon occurred in *K. japonica*. The origin of binucleate mycelium at an early stage of infection by a uninucleate basidiospore, as suggested by Jackson (1931), can be attributed to this mode.

5. Fusion of compatible spermatia with receptive hyphae in the spermogonium

The function of spermatia in spermogonia in the sexual reproduction of rust fungi was first proven by Craigie (1927a,b), who undertook intensive crossing experiments with *P. helianthi* and *P. graminis*. From the results he obtained, Craigie (1927a,b) deduced that hyphae and spermatia in the spermogonium were female and male gametes, respectively, which were produced by two sexually different types of basidiospores, and concluded that the vegetative mycelium and subsequent aeciospores were produced only when the fusion of spermatia of one sexual type with hyphae of another sexual type occurred in the spermogonium. In controlled experiments, he also deduced that insects would play an important role in cross-spermatization in nature.

Thereafter, sexual reproduction by cross-spermatization in the spermogonia has been reported across macrocyclic rust species, e.g., *Puccinia triticina* Eriks. (= *P. recondita* Desm) (Allen 1932), *P. sorghi* Schwein. (Allen 1933), *P. phragmitis* (Schum.) Körn (Lamb 1935), *P. anomala* Rostr. (= *P. hordei* Oth), *P. coronata* Corda, *Uromyces appendiculatus* (Pers.) Unger, *U. vignae* Barclay, *U. graminis* (Niessl) Dietel, *U. trifolii-hybridi* H.G.K. Pau (= *U. trifolii-repentis* Liro), *U. fabae* de Bary (= *U. viciaefabae* J. Schröt.), *Gymnosporangium haraeaeum* Syd. & P. Syd. (= *G. asiaticum* G. Yamada), *G. juniperi-virginianae* Schwein., *G. globosum* Farl., *Cronartium ribicola* J. C. Fischer, *Melampsora lini* (Eremb.) Lév. (last 13 species cited from Brown 1940), and many other macrocyclic or demicyclic species.

6. Fusion of spermatia with stomatal hyphae (Andrus 1931; Allen 1934)

Andrus (1931) reported, in *U. appendiculatus* and *U. vignae*, that a uninucleate mycelium in an aecial primordium was dikaryotized by fusion of spermatia with receptive hyphae that emerged through the host epidermis. However, conclusive evidence to support this perspective is needed (Olive 1953).

7. Germination of spermatia and entrance of the germ tube through a stoma "to become effective" (Allen 1934)

Conclusive evidence to support this method is lacking (Olive 1953). Budding of spermatia in *Coleosporium tussilaginis* (Pers.) Lév. was once reported (Deml et al. 1982); however, it was found that the reported observation was based on nonrust yeasts (Bauer 1986).

8. Fusion of spermatia in pairs (Allen 1934)

No conclusive evidence to support of this method is available (Olive 1953).

Heterothallism

As listed in the mode of dikaryotization 4 (fusion of compatible spermatia with receptive hyphae in the spermogonium), many, probably most, macrocyclic and demicyclic species with spermogonia in the life cycle would prove to be heterothallic. Contrary to macrocyclic species, few cases have been documented in which dikaryotization, either between compatible spermatia and receptive hyphae in the spermogonium or between compatible vegetative mycelia, is prerequisite for the development of teliospores.

In *P. prostii* (Lamb 1934; Olive 1953), the dikaryotic condition is reported to arise at the base of a telium primordium, either by means of cell fusion or by nuclear migration, and this species is suspected to be heterothallic. *Puccinia pampeana* produces both *Endophyllum*-type and *Puccinia*-type teliospores, only after cross-spermatization in the spermogonium (Hennen et al. 1984). Without cross-spermatization, the systemic infection forming the spermogonium remains so for a considerable period of time. The result indicates the heterothallic nature of sexual reproduction in this species. *Endocronartium sahoanum* var. *sahoanum* (Imazu et al. 1989), *E. sahoanum* var. *hokkaidoense* (Imazu and Kakishima 1992), and *E. yamabense* (Saho & I. Takah.) Paclt (Imazu et al. 1991a,b) are suggested be heterothallic.

Homothallism

The diverse modes of nuclear behavior and accompanying morphological change in metabasidium and basidiospore production, as described here, clearly indicate that a large number of microcyclic rust fungi are either homothallic, when reproducing sexually, or apomictic or asexual in their reproduction. Nevertheless, homothallism has been proven by a single basidiospore inoculation only in the following species: *P. malvacearum* (Ashworth 1931), *P. mesnieriana* (Anikster and Wahl 1985), *K. japonica* (Ono 2002), *U. aloes* (a single teliospore inoculation; Thirumalachar 1946), *U. viennot-bourgini* (Anikster et al. 1980), and *U. scillarum* f. sp. *leopoldiae-maritimae* (Anikster et al. 1980).

Variants in the type I nuclear cycle indicate that many microcyclic rust fungi have become homothallic and have

simplified the nuclear cycle and associated sexual structures during their evolution. During the course of life cycle reduction and the simplification of the sexual process, most microcyclic rust fungi seem either to have lost spermogonia entirely or their function where the spermogonia are still formed. For this reason, Buller (1950) and others believed that the absence or imperfect development of spermogonia indicates the homothallic nature of the sexual reproduction in microcyclic rust fungi.

Buller (1941) distinguished two kinds of homothallism in fungi: “haplomonocious” homothallic, where the life cycle starts with a single uninucleate basidiospore, and “miktohaplontic” homothallic (sexually heterokaryotic; secondarily homothallic), where a basidiospore is bisexual, containing the nuclei of both sexes. In those species whose basidiospores are produced on a two-celled metabasidium and contain two nuclei (meiotic diads), the two nuclei may be homokaryotic or heterokaryotic at any given gene locus, depending on the segregation of the genes over the two divisions (Petersen 1974), and may be homothallic or secondarily homothallic. Both kinds of homothallism commonly exist among microcyclic rust fungi, which include *K. japonica* (Ono 2002), *P. anemones-virginianae* (Jackson 1935), *P. arenariae* (Lindfors 1924), *P. circaeae* (Ono 2003), *P. grindeliae* (Brown 1940), *P. heucherae* (Jackson 1935), *P. horiana* (Kohno et al. 1974, 1975a), *P. malvacearum* (Blackman and Fraser 1906; Ashworth 1935), *P. mesnieriana* (Anikster and Wahl 1985), *P. rutainsulara* (Gardner 1994), *P. xanthii* (Brown 1940), *U. aloes* (Thirumalachar 1946), *U. alyxiae* (Gardner 1987), *U. oliveirae* (Anikster et al. 1980), nine formae speciales of *U. schillarum* (Anikster et al. 1980), *U. viennot-bourginii* (Anikster et al. 1980), *E. heliotropii* (Thirumalachar and Narasimhan 1950), and *C. weirii* (Crane et al. 2000).

Homothallism generally implies the genetic homogeneity of the fungal population; however, it does not prevent but reduces the frequency of outcrossing in the population (Carlile 1987). When two homothallic populations of different genotypes are brought together, heterokaryosis and the heterozygous condition at any gene locus are expected by infection of the basidiospores of two genetically different populations. Karyogamy and subsequent meiosis result in nuclei of different genetic constitution through a random assortment of homologous chromosomes.

Even in a single population, two haploid nuclei in the mycelium become genetically different if gene or chromosomal mutations occur in either one or both nuclei. Uninucleate basidiospores originated from heterokaryotic mycelium thus formed are different genetically and may infect a plant in sufficiently close proximity. The infection hyphae derived from the two basidiospores may result in heterokaryosis and heterozygosity in a new generation of the population that had been homozygous. Through these processes, genetic diversity might have been and would be maintained even in the homothallic microcyclic rust fungi. Olive (1953) predicted that heterokaryosis, heterozygosity, and segregation would be found to occur quite commonly among homothallic rust fungi.

Apomixis

Sexual recombination is a widespread phenomenon in eukaryotic organisms. It is often believed that sex promotes genetic variability and that sexually reproducing organisms evolve faster than asexually reproducing ones (Barton and Charlesworth 1998). The common occurrence of sex among eukaryotic organisms suggests the existence of strong driving forces that favor the evolution and persistence of sex (Maynard Smith 1978; Wuerthrich 1998). However, sex still maintains uncertainty or inherent disadvantages in evolution (Maynard Smith 1978; Barton and Charlesworth 1998): it is not certain a priori that heritable variance in fitness is significantly increased by sex; sexual recombination would break up adaptive gene complexes that have been established through natural selection; and sexually reproducing organisms must allocate much resource to reproductive organs. Consequently, in environments where sex does not significantly increase fitness or genetic recombination breaks up adaptive gene complexes, apomictic or vegetative reproduction would have been favored.

This scenario can be applied to rust fungi. The apomictic reproduction has been proven in *P. lantanae* (Ono 2002) by cytology and artificial inoculations and assumed in the following rust fungi: *P. patriniae* (Ono 2002), three endocyclic forms of *U. hobsoni* (Payak 1953), *U. rudbeckiae* (Olive 1911; Jackson 1931), a binucleate form of *G. nitens* (Kunkel 1914; Dodge and Gaiser 1926; Dodge 1929; Olive 1953), a small uninucleate form of *G. nitens* (Dodge 1924, 1929; Jackson 1935; Olive 1953), *E. centranthi-rubri* (Poirault 1913, 1915; Jackson 1935), a uninucleate form of *E. euphorbiae-sylvaticae* (Moreau 1911, 1914, 1915; Moreau and Moreau 1918a, 1919; Dodge 1929; Olive 1953), a binucleate form of *E. euphorbiae-sylvaticae* (Sappin-Trouffy 1896; Moreau 1911, 1914, 1915; Moreau and Moreau 1918a, 1919; Dodge 1929; Olive 1953), *E. heliotropii* (Thirumalachar and Narasimhan 1950), *E. spilanthes* (Thirumalachar and Govindu 1954), *E. valerianae-tuberosae* (Maire 1900; Poirault 1915; Jackson 1931, 1935), and *P. yamabense* (Hiratsuka 1986).

In rust fungi, through the evolution of apomictic reproduction, metabasidia and basidiospores might have been so simplified that they can hardly be distinguished from a germ tube or infection hypha arisen from vegetative spores.

Secondarily asexual reproduction

It is highly likely that many unconnected *Aecidium*, *Peridermium*, *Roestelia*, and *Caeoma* species have the entirely haploid binucleate condition without a sexual stage in the life cycle. Wholly asexual reproduction with an aeciospore-type of vegetative spores has been confirmed by cytology and artificial inoculations in such anamorphic fungi as *A. mori* (Kaneko 1973), *A. raphidolepidis*, and *A. portheriae* (Sato and Sato 1981), *P. harknesii* (Epstein and Buurlage 1988; Vogler et al. 1997), and *P. pini* (Gibbs et al. 1988). Hantula et al. (2002) suggested by molecular genetic analyses that *P. pini* had originated from sexually reproduc-

ing *Cronartium flaccidum* (Alb. & Schwein.) G. Winter. These examples suggest reduction of life cycle to the ultimate vegetative reproduction through the endophylloid pathway, i.e., conferring the function of a telial stage to an aecial stage of macrocyclic parental species, as advocated by Hennen and Figueiredo (1984).

The foregoing discussion does not exclude the possibility that truly vegetative reproduction by urediniospores could have been evolved by omission of spermogonial, aecial, and telial stages in the life cycle. Many unconnected *Uredo* species would be proven as truly asexual "species."

Ecological and evolutionary significance of homothallism, apomixis, and asexuality in microcyclic rust fungi

A number of data have indicated that microcyclic rust fungi have become homothallic, apomictic, or asexual in reproduction during the course of life cycle reduction. The development of homothallism during the evolution of microcyclic rust fungi, mostly from macrocyclic heteroecious parental species (Jackson 1931), may bear special importance in their biology.

In examining rust-infected plant materials from northwestern Greenland, Arthur (1928) noticed that most common rust fungi observed there are microcyclic in the life cycle and that those rust fungi that possess a macrocyclic heteroecious life cycle persist by a uredinial stage, whose mycelium survives in the host tissue for a considerable period of time. In the study of rust flora in the alpine region of Japan, Hiratsuka (1935) showed that the number of microcyclic rust fungi increase with the increase of latitude of localities and altitude of mountains and that 35 species (~42%) of 83 species found in the alpine regions were microcyclic.

Savile (1953) also noticed that microcyclic rust fungi, which seem self-fertile, are prevalent in the arctic region in northern Canada and that many heteroecious species persist by a uredinial stage or an aecial stage, whose mycelium overwinters in evergreen host tissues. Savile (1953, 1976) believed that facultative or permanent reduction of life cycle and self-fertility are an effective adaptation to a short growing season.

After having become macrocyclic, either autoecious or heteroecious, teliospores in many rust fungi have become deciduous, acquiring a function of dissemination with increased wall thickness and melanization. For those rust fungi, vegetative reproduction by aeciospores and urediniospores is not economical under severe ecological conditions where their hosts are scattered and the suitable growing period is short. Under such conditions, aeciospores and urediniospores are not functioning, i.e., no new infection by those spores will result in effective reproduction in places where potential hosts are not easily available and the favorable climate persists for only a short period. Production of highly tolerant and migratory teliospores is the most economical and safest way of life and, to become so, the

acquisition of self-fertility becomes prerequisite. On the other hand, a totally clonal life cycle with repeating aeciospores or urediniospores would also be highly adaptive as well.

Similar interpretation has been presented for the prevalence of short-cycled, self-fertile *Uromyces* species (Anikster et al. 1980) and *Puccinia mesnieriana* (Anikster and Wahl 1985) in Israel, where the rust fungi must survive a short growing season under the semiarid climatic condition.

These observations and interpretations suggest that homothallic, apomictic, or vegetative reproduction is highly adaptive for rust fungi inhabiting severe ecological conditions and that homothallic, apomictic, or asexually reproducing variants could have been selected from heterothallic macrocyclic parental species under such adverse conditions. Some of the incipient populations of reduced life cycle derived from parental populations might have succeeded to become distinct species whereas most might have become extinct under still harsh conditions.

Brasier (1987) presented, with some convincing examples of plant pathogenic fungi, a possible mode of the speciation of clonal or self-fertile populations in response to severe ecological disturbance ("episodic selection"). Under a severe ecological condition, a genetically uniform population may arise from an originally variable population by reduction or loss of outcrossing ability or acquisition of self-fertility. If episodic selection continues and if a reproductive isolating mechanism develops, the self-fertile or clonal populations would rapidly speciate. If the speciating populations enter the narrow and recurrently distributed niche where the populations are partitioned in a small size, the population would become a self-fertile or vegetatively reproducing species.

As in vascular plants (Barton and Charlesworth 1998), secondary asexuality can evolve in fungi independently many times at different localities. The evidence seems to support the possibility of multiple origins of microcyclic or clonal rust lineages from the same ancestral rust species.

It is readily accepted that asexually reproducing rust fungi persist for much shorter periods in evolutionary time than their sexually reproducing relatives (Maynard Smith 1978; Barton and Charlesworth 1998). Buller (1950) pointed out that the advantage of life cycle reduction with a short generation time was gained at the cost of reduced genetic variability, which eventually leads to evolutionary stagnancy. That apomictically or vegetatively reproducing species are widespread, particularly in cool temperate and arctic regions, however, indicates that a dynamic equilibrium between extinction and reestablishment of microcyclic or asexual species exists as a common evolutionary phenomenon among the rust fungi. Repeated derivation of microcyclic lineages from macrocyclic parental species might have compensated the extinction in the past evolutionary history.

The *Gymnoconia nitens* species complex, the *E. euphorbiae-silvaticae* species complex, the *U. hobsoni* species complex, the *C. flaccidum*-*E. pini*-*P. pini* complex, the *C. coleosporioides*-*E. harknesii*-*P. harknesii* complex, and

the *C. ribicola*–*E. yamabense*–*P. yamabense* complex may represent examples of repeated derivation of microcyclic or clonal populations in different times and places. Because of the possibility of independent evolution, these morphologically delimited microcyclic or clonal species may consist of populations that are heterogeneous in terms of nuclear behavior and genetic constitution.

In addition to the mode of adaptation under cold environmental conditions, through which apomictically or asexually reproducing rust fungi evolved, there is another possibility that microcyclic species with similar reproductive traits have evolved under warm and humid climatic conditions or “mild and stable” ecological conditions. After having become macrocyclic, either autoecious or heteroecious, certain rust fungi might have entered mild and stable environments where conditions are favorable for continuous growth and reproduction and the hosts are almost always available throughout the year. Under those stable and favorable environmental conditions, the production of pleomorphic spores might be redundant. Allocation of available resources to the vegetative mycelium and one kind of spores might have been favored. The spores produced might be sexual, apomictic, or clonal in their genetic nature. Those fungi that have deleted aecial and uredinial stages from the life cycle seem to have the highest selective advantage. Those rust species that produce only teliospores that germinate without dormancy to initiate new generations repeatedly in a single growing season would be highly adaptive. *Puccinia pampeana*, *U. alyxiae*, *P. rutainsulara*, *P. rugispora*, *P. vittata*, *E. acaciae*, *E. hawaiiense*, and *Monosporidium machili* and many other tropical *Endophyllum* species might represent these microcyclic species.

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