

Eucalyptus Rust: A Disease with the Potential for Serious International Implications

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ABSTRACT

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Eucalyptus spp. are propagated extensively as non-natives in plantations in many parts of the tropics and sub-tropics. A number of diseases result in serious losses to this economically important forest resource. Eucalyptus rust, caused by *Puccinia psidii*, is one such example. The economic losses due to this disease are the result of infections of seedlings, young trees, and coppice. *P. psidii* occurs predominately in Central and South America, but reports of a similar rust are known from other areas. Eucalyptus rust is a remarkable disease in that the pathogen is not known on eucalypts in their centers of origin. It has apparently originated on native Myrtaceae in South America and is highly infective on some *Eucalyptus* spp. planted there. *P. psidii* causes one of the most serious forestry diseases in Brazil and is considered to be the most serious threat to eucalypt plantations worldwide. Advances in eucalyptus rust research are reviewed here, with a focus on topics such as distribution, host range, pathogen specialization, symptomatology, etiology, epidemiology, and control.

The Myrtaceae family includes a number of economically important tree crops, notably *Eucalyptus* spp., *Psidium guajava*, *Pimenta officinalis*, and *Syzygium aromaticum*. The greater portion of this family occurs in the Australasian and Southeast Asian regions, and in Central and South America, with four genera native to southern Africa (35,49,55). Of the economically important tree crops, *Eucalyptus* spp. are most significant and make up over eight million hectares of forest plantations in the tropics and sub-tropics (52). Diseases are thus considered to be a major threat to this forestry resource (57).

During the course of the past century, a number of genera and species of rust fungi have been reported to infect members of Myrtaceae. The majority of these species belong to the genus *Puccinia* Pers., while others are found in the genera *Aecidium* Pers., *Caeoma* Link, *Melampsora* Castagne, *Uredo* Pers., and *Uromyces* (Link) Unger (51). Further

taxonomic investigations have, however, led researchers to synonymize many of these genera (29,54).

Many of the rust fungi naturally infecting Myrtaceae occur on a wide variety of hosts. *Puccinia psidii* Winter is the only rust confirmed to be capable of infecting *Eucalyptus* spp. This fungus has also been reported to infect 10 other genera of Myrtaceae. The pathogen was first described by Winter (58) in 1884 on *Psidium pomiferum* in Brazil. In 1912, it was observed on *Eucalyptus citriodora* (26) but was not formally described from this host until 1944 (29). The first serious outbreak of *P. psidii* on a *Eucalyptus* sp. occurred in 1973 in the Brazilian province of Espírito Santo, where large-scale losses were experienced in nurseries and young plantations of *E. grandis* established from South African seed sources (20,21).

Puccinia psidii is currently a serious threat to eucalyptus plantations in many parts of the world, and particularly in Australia, where eucalypts are native. Considering the serious nature of eucalyptus rust and its international importance, this review is provided for a wider literary audience. Ferreira (21,23) published reviews on the history, biology, and control of eucalyptus rust in Portuguese. Here we discuss advances in research on topics relating to its distribution, host range, pathogen spe-

cialization, symptomatology, etiology, epidemiology, and disease control.

Distribution. *P. psidii* has been reported from South America (Argentina, Brazil, Colombia, Ecuador, Paraguay, Uruguay, and Venezuela), Central America, the Caribbean (Cuba, Dominican Republic, Jamaica, Puerto Rico, and Trinidad) (32), and South Florida (34). A rust, suggested to be *P. psidii*, has recently also been reported from Taiwan on *E. camaldulensis* (56). In this case, only a uredinial state was reported and it is impossible to confirm whether the fungus was the same as *P. psidii*. Despite considerable effort, the fungus has not been seen again (W. Wang, Taiwan Forestry Research Institute, per-

Table 1. List of reported hosts of *Puccinia psidii*; all belong to the family Myrtaceae

Host	Reference
<i>Callistemon speciosus</i> (Sims) DC	32
<i>Eucalyptus camaldulensis</i> Dehnhardt	19
<i>E. citriodora</i> Hook.	26
<i>E. cloeziana</i> F. Muell.	19
<i>E. grandis</i> Hill ex Maiden	20
<i>E. maculata</i> Hooker	19
<i>E. microcorys</i> F. Mueller	19
<i>E. paniculata</i> Sm.	19
<i>E. pellita</i> F. Mueller	19
<i>E. phaeotricha</i> Blakely et Mckie	19
<i>E. pirocarpa</i> L. Johnson, D. Blaxell.	19
<i>E. punctata</i> De Condolle	19
<i>E. saligna</i> Smith	21
<i>E. tereticornis</i> Sm.	19
<i>E. urophylla</i> S.T. Blake	19
<i>Eugenia brasiliensis</i> Lam.	53
<i>E. jambolana</i> Lam.	53
<i>E. malaccensis</i> L.	32
<i>Eugenia</i> sp.	54
<i>E. uniflora</i> L.	53
<i>E. uvalha</i> Camb.	32
<i>Marierea edulis</i> Niedz	54
<i>Melaleuca leucodendron</i> (L.) L.	54
<i>Myrcia jaboticaba</i> Berg	54
<i>Myrcia</i> spp.	32
<i>Myrciaria</i> sp.	54
<i>Pimenta acris</i> Kostel	32
<i>P. dioica</i> (L.) Merr.	34
<i>P. officinalis</i> L.	3, 33
<i>Psidium araca</i> Raddi	54
<i>P. guajava</i> L.	58
<i>P. pomiferum</i> L.	58
<i>Syzygium jambos</i> (L.) Alston	32

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sonal communication). Another rust infecting *Eucalyptus* spp. has been reported from India, where it was identified as a species of *Melampsora* (53). Type material of the latter fungus has, however, failed to reveal whether this identification was correct (I. Gibson, personal communication). Recently, Knipscheer and Crous (30) reported a rust on *E. nitens* in South Africa. This fungus was not successfully identified to genus, due to the absence of teliospores, and it has subsequently disappeared from forest plantations.

Host range and pathogen specialization. *P. psidii* is capable of infecting many

species in the Myrtaceae (Table 1; Fig. 1A and B). This fungus was originally described from infected *P. pomiferum* leaves (58) and, in 1904, Sydow and Sydow (51) listed only *Psidium* spp. as hosts. Arthur (4,5) and Stevenson (50) listed only *P. guajava* and *S. jambos* as hosts, but Joffily (29), Viégas (54), and Laundon and Waterston (32) listed several other genera as hosts of *P. psidii*. Joffily (29) and Viégas (54) considered several of the rusts described on various genera of Myrtaceae as not being distinct from *P. psidii*. Their conclusions were not based on detailed taxonomic studies, and until such a study is

complete, the host range of *P. psidii* will remain enigmatic.

Cross-inoculations among hosts indicate that there is considerable physiological variability within *P. psidii* (7,8,12,14,20,23,33). Ferreira (23) suggested that the host range has expanded within the Myrtaceae family. He speculated that the wild ancestor of *P. psidii* was able to infect a number of species, such as *S. jambos*, *Eucalyptus* spp., *Myrcia jaboticaba*, *Calistemon speciosus*, and wild and commercial varieties of *P. guajava*. Reciprocal cross-inoculations among these hosts were performed (23), and it was found that only

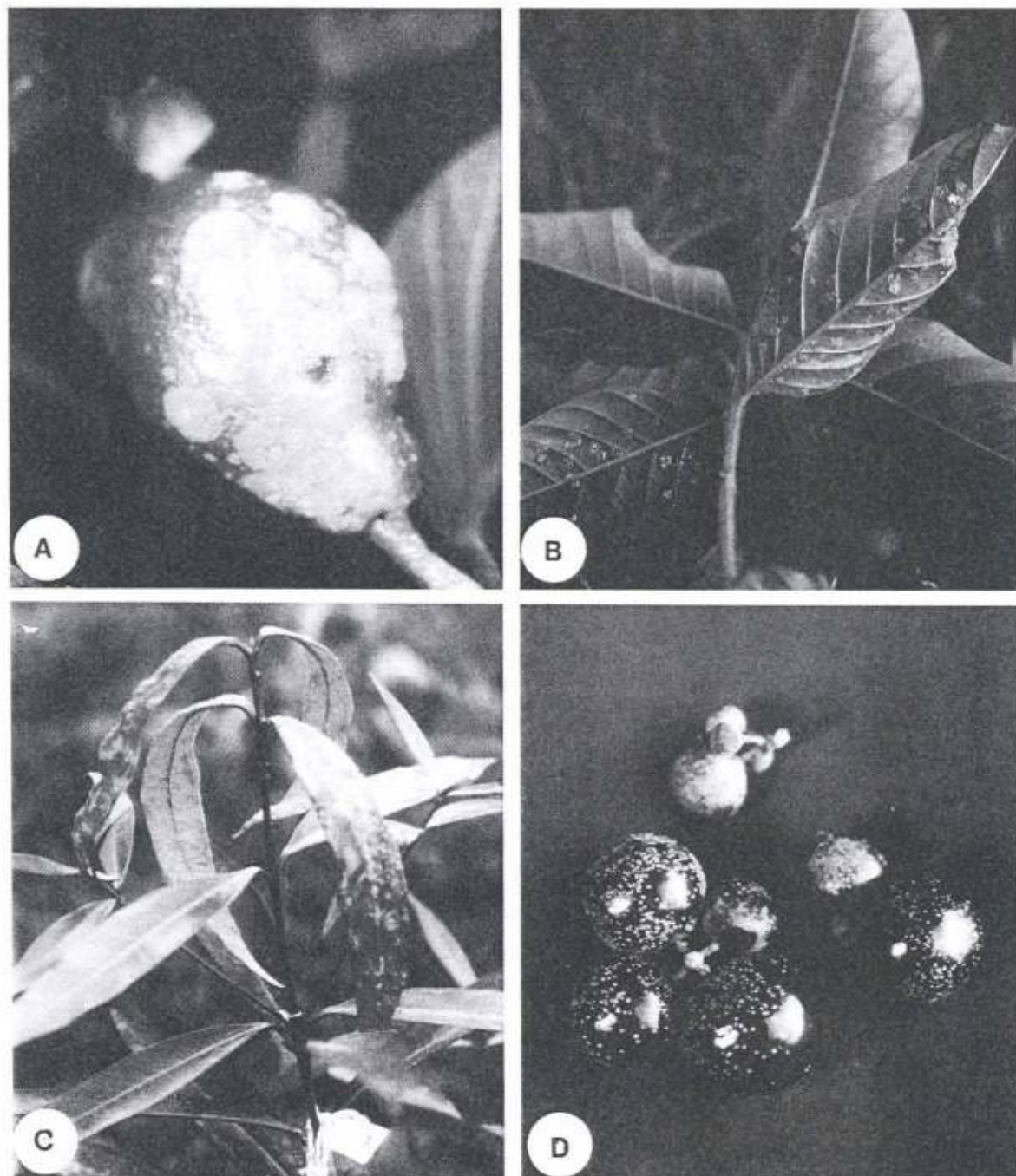


Fig. 1. Pustules of *Puccinia psidii* on different hosts. (A) *Psidium guajava* fruit. (B) *P. guajava* leaves. (C) *Syzygium jambos* leaves. (D) *Myrcia jaboticaba* fruit.

the urediniospores collected from the wild and commercial *P. guajava* were incapable of infecting the other species. Castro et al. (12,15) reported that spores collected from *P. guajava* were able to infect various clones of *E. grandis*. Coelho (7), in a cross-inoculation study with single pustule isolates from *Eucalyptus* spp., *P. guajava*,

and *S. jambos*, reported that there are three physiological groups of *P. psidii*. Group 1 infects *Eucalyptus* spp. and *S. jambos*, Group 2 infects *Eucalyptus* spp. and *P. guajava*, and Group 3 is able to infect *P. guajava* only. The apparent contradiction in the results obtained by the researchers who have conducted cross-inoculation

studies may be due to race differences within *P. psidii*. Races or formae speciales of this pathogen have yet to be described, but as is the case with other rust fungi, such as coffee rust (*Hemileia vastatrix* Berk. & Br.; 6), they seem likely to exist.

Symptomatology. *Eucalyptus* spp. are most susceptible to infection by *P. psidii*

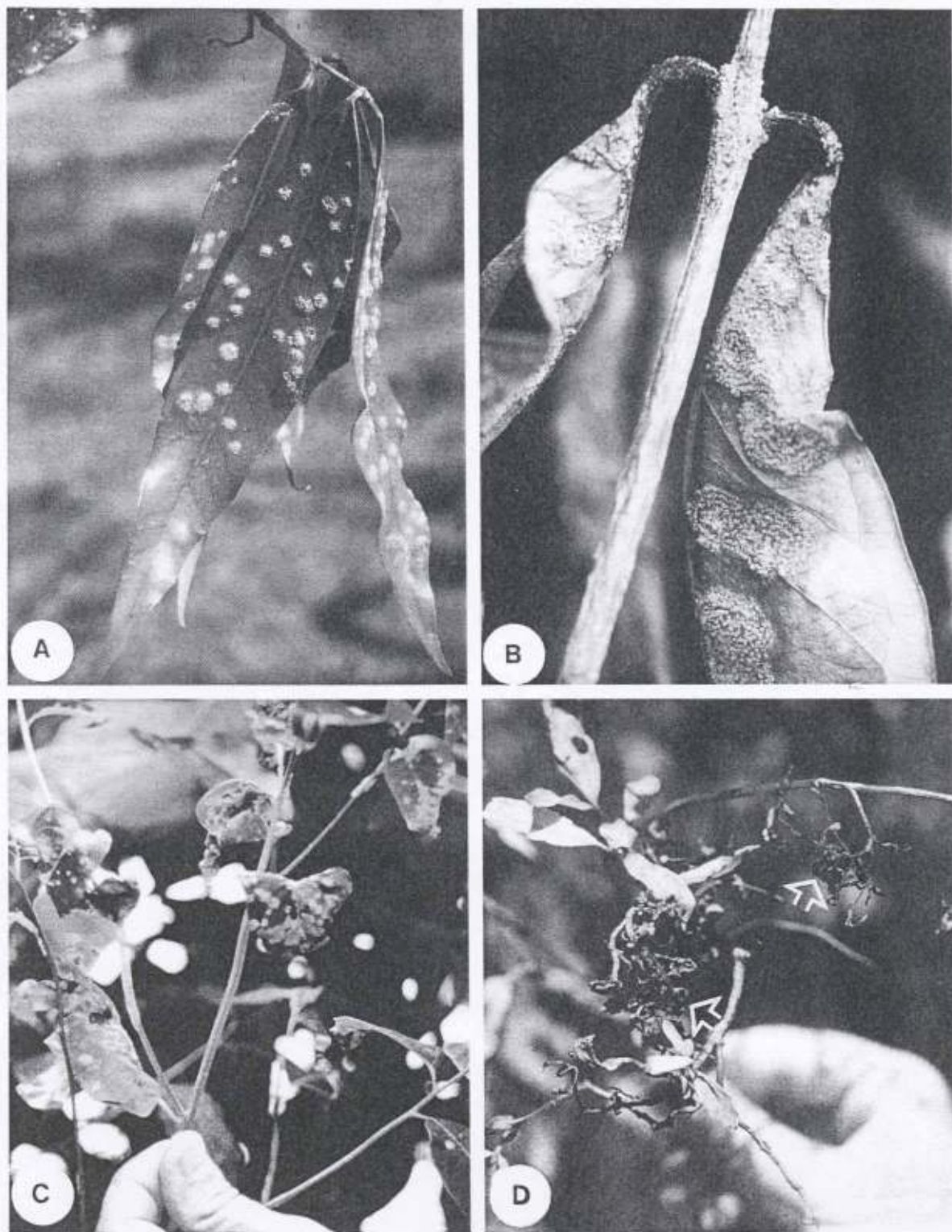


Fig. 2. Symptoms of eucalyptus rust on *Syzygium jambos* and *Eucalyptus* spp. (A) The characteristic egg-yolk yellow pustules on *S. jambos* leaves. (B) Stem and leaves of *S. jambos* showing the coalescence of uredinia. (C) Infection of the stem and leaves of *Eucalyptus* sp. showing the coalescence of pustules, necrosis, and hypertrophy. (D) Tip die-back (arrows) of *E. grandis* following infection.

when they are less than 2 years old (3,20,21). The first symptoms of eucalyptus rust become visible 2 to 4 days after the host has been inoculated with urediniospores (23). According to Ferreira (21) and Alfenas et al. (2), the first evidence of attack by this fungus is the appearance of pale yellow specks on the leaf buds. Within 10 to 12 days after inoculation with urediniospores, the specks deepen in color to a characteristic egg-yolk yellow and uredinia become visible under a dissection microscope (Fig. 2A). Thereafter, the infected areas increase in size in a circular manner due to the radial growth of the fungus. Infected areas often coalesce with age (Fig. 2B). Secondary infections occur within a few days and are confined to new plant tissues, such as primordial leaves, their petioles, and branch tips. In severe cases, the main and secondary juvenile branches of young plants are attacked (Fig. 2C). When the tissue is susceptible, the infected parts of the tree shrivel and die (Fig. 2D).

When leaves that have reached 50% of their full growth are infected by *P. psidii*, less intense sporulation is displayed and is usually restricted to the lower leaf surfaces (23). Pustules in this case are generally confined to areas between the veins, and the leaves are often deformed. Sporulation of *P. psidii* on infected parts of seedlings ceases after 2 weeks. Tips of branches and the main stem then display hypertrophy and diagnosis becomes difficult. Eucalypt-

tus rust rarely kills its host, except when it is found on coppice growth of highly susceptible *Eucalyptus* spp. Plants recover by producing new growth that may become infected if the conditions are favorable. If the trees are continuously re-infected they become stunted (45).

Life cycle. The life cycle of *P. psidii* remained unknown until the early 1980s. It has since been discovered that this fungus has a macrocyclic life cycle (Fig. 3). The following states occur: aecia (state 1), uredinia (state 2), telia (state 3), and basidia (state 4; 23,33). Spermatia (state 0) have not as yet been found (23), but due to the reported occurrence of aecia (25) this stage must exist. This fungus is also considered to be autoecious (25).

The only study conducted on the morphology of the different stages in the life cycle of *P. psidii* is one described by Ferreira (23). Teliospores are dark brown in color and are pedicellate, bicellular, and club-shaped, with a flattened papilla on the wall distal to the pedicel cell (15 to 28 by 30 to 60 μm ; Fig. 4A). Pustules may consist of a mixture of teliospores and urediniospores, but these spore types may also be produced in telia (Fig. 4B) and uredinia (Fig. 4C) only. Either one or both cells of the teliospore germinate to form basidia under humid conditions. A very low percentage (8%) of teliospores is reported to germinate (9). Basidia are 40 to 70 μm in length and only 0.1% produce basidio-

spores, which are borne on sterigmata (23). Aeciospores have the same morphology as urediniospores. The shape of both spore types is variable; they may be pyriform to spherical or oval with angular outer walls (10 to 20 by 15 to 25 μm ; Fig. 4D). Aeciospores have been found only on *S. jambos* (25).

Teliospores and basidiospores are seldom found on naturally infected eucalyptus trees (21). However, Ruiz (38) reported that teliospores occur under natural conditions in Brazil on *E. cloeziana* during the warmer months of the year (December to March). They are, however, frequently found on *S. jambos* and occasionally on *M. jabaticaba* under natural conditions. Many teliospores are produced on artificially inoculated *Eucalyptus* spp. and *S. jambos* (38). Basidiospores have been shown to infect only *S. jambos*, and then only at temperatures greater than 25°C (25). Aeciospore formation usually occurs 10 to 18 days following infection (25).

Infection process. In the presence of free water, in darkness, and at temperatures between 15 and 25°C, urediniospores germinate on the host surface (11,16,23, 37,40,44,46). In Brazil, these ideal environmental conditions are experienced from May to August, and the highest levels of rust were recorded during this period (19,43,45). However, favorable periods for infection may vary from year to year and according to the geographic region. Light

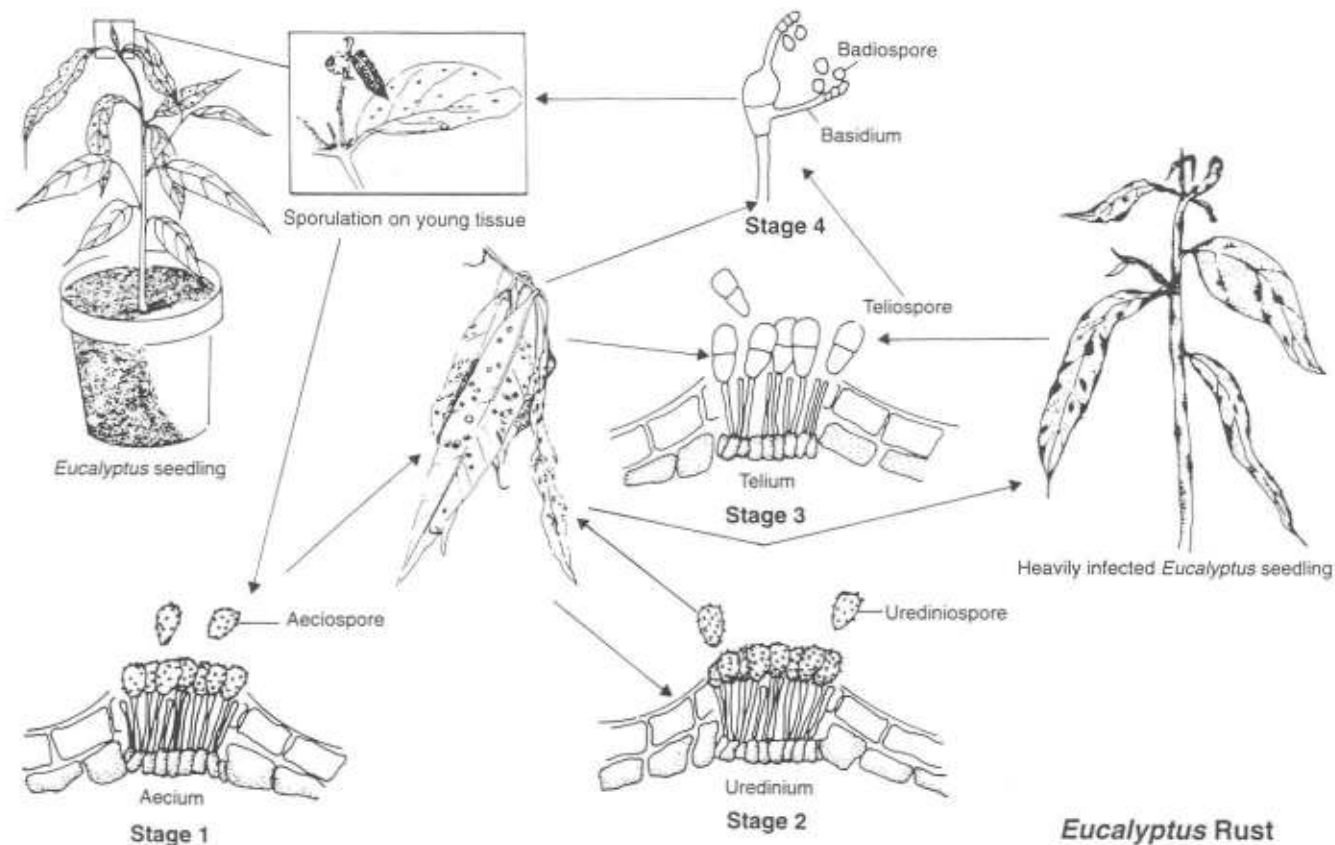


Fig. 3. Diagrammatic representation of the life cycle of *Puccinia psidii*.

has been found to inhibit germination (46,47) and at least 8 h of darkness are required for successful infection (36). In an infection study conducted by Hunt (28) on *S. jambos* inoculated with *P. psidii* urediniospores, the following was observed: a single, unbranched germ tube was formed, a thin-walled, globose or ellipsoidal appressorium developed from the tip of the germ tube, and an infection peg penetrated the host directly (Fig. 4E). Penetration usually took place between two epidermal cells or, less commonly, in the corners between three epidermal cells. This penetration procedure has been observed on hosts other than *S. jambos*, including *Eucalyptus* spp. (23). Urediniospore germ tubes of only a few rust fungi are capable of direct penetration (28). *H. vastatrix*, for example, relies on stomata for entry into the host (27).

Studies on the host-pathogen interaction between *P. psidii* and *Eucalyptus* spp. con-

ducted in Brazil have shown that urediniospores germinate on both young and mature leaves of susceptible and resistant genotypes (A. Xavier, A. C. Alfenas, and K. Matsuoka, unpublished data). On mature leaves of *Eucalyptus* spp., germination is retarded and the number of appressoria formed is much lower than on juvenile leaves. Direct penetration occurs on young leaves of both resistant and susceptible genotypes within 24 h after inoculation. In resistant genotypes, the haustoria formed within the host cells and the surrounding cells underwent a hypersensitive reaction and collapsed. Following penetration on the susceptible genotype, the fungus ramifies intercellularly through the host tissue. A temperature of 15°C has been found to promote mycelial growth within the host (23). Haustorium mother cells are formed from the infection hyphae (23); from these cells, lobe-shaped haustoria then formed

within the host cells. Germ tubes of basidiospores and aeciospores are also reported to penetrate the host directly (25).

In incompatible reactions, either as a result of infection of a non-host or a resistant host, punctate, atypical pustules are formed on the broadest part of the leaf (24). These pustules are smaller in size, and sporulation takes place only in the center of the infected area. Fewer "normal" pustules are formed on the incompatible tissue. A hypersensitive reaction (7,23), which results in the death of a few cells at the site of penetration, has also been observed.

Epidemiology. The fungus has a latent period, from the beginning of incubation to the time at which 50% of the first uredinia appeared, of 5 to 7 days (1). This is considerably shorter than, for example, the latent period of *H. vastatrix*, which ranges from 30 to 60 days (10). Castro et al. (13) showed that most urediniospores of *P.*

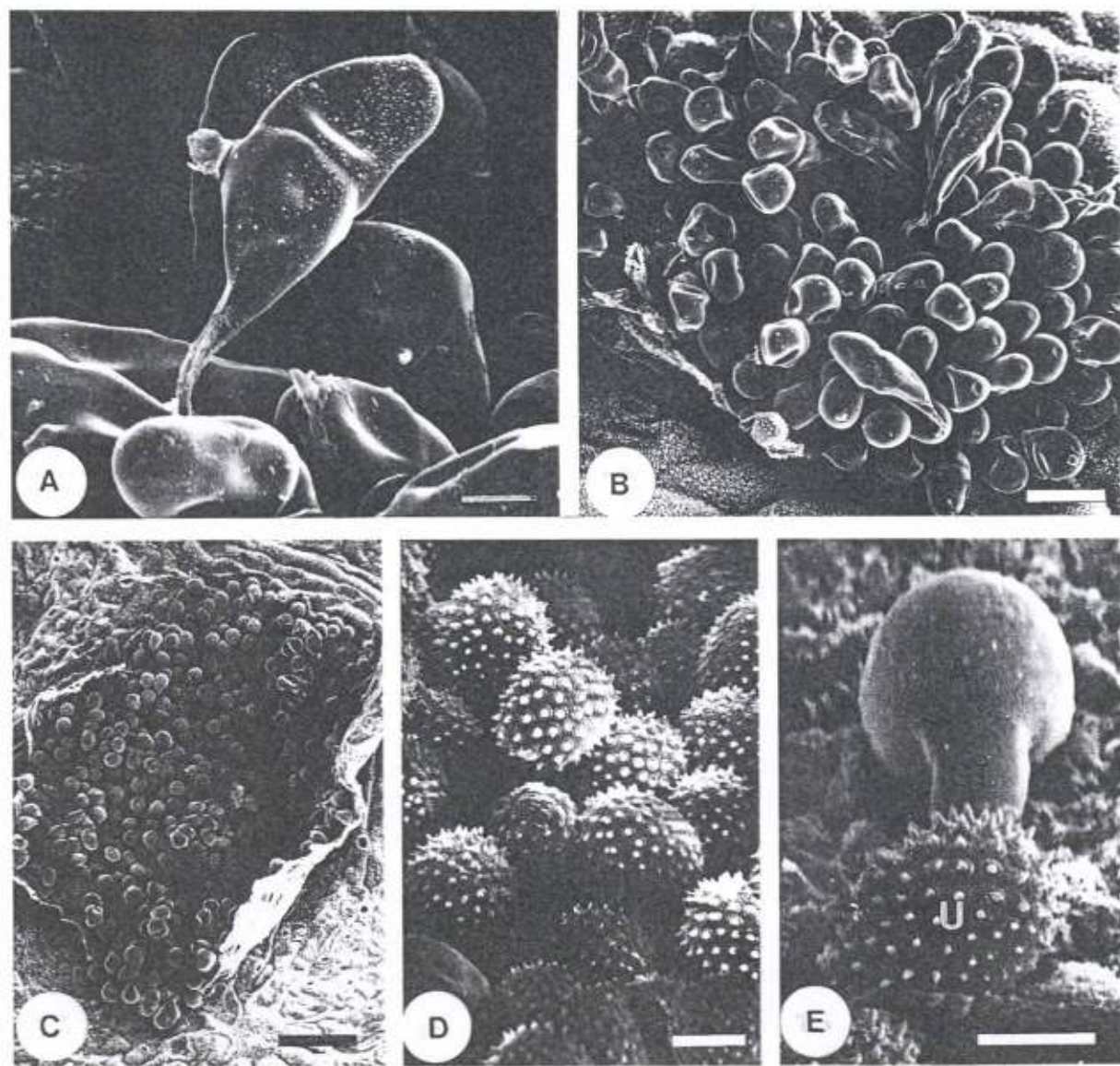


Fig. 4. Scanning electron micrographs of the spore types and infection process of *Puccinia psidii* on *Eucalyptus* sp. leaves. (A) Two-celled teliospores (bar 10 μ m). (B) Telium (bar 20 μ m). (C) Uredinium (bar 100 μ m). (D) Single-celled urediniospores (bar 10 μ m). (E) Urediniospore (U), germ tube (GT), and appressorium (A) on the leaf surface (bar 20 μ m).

psidii are produced within the first 10 days after infection, although the number of urediniospores did depend on the host.

Temperatures of 15 and 30°C inhibit uredinial sporulation (42). The ideal temperature for the generation of urediniospores of *P. psidii* has been found to be 20°C (20). Infected plants maintained at 25°C are more likely to produce telia than uredinia (42). Light, following the incubation period, enhances the production of both telio- and urediniospores (42,47).

After the first uredinial pustules appear, secondary infections arise on host tissue. The urediniospores from these pustules spread to susceptible tissue by rain, insects, and wind (21). It has been suggested that primary infections result from inoculum originating from hosts other than eucalypts, or from basidiospore/aeciospore infection (21).

Control

Three methods are recommended for disease control: disease avoidance, planting resistant genotypes, and fungicide applications. The latter strategy, however, is practical only in nursery situations and on coppice (2).

Disease avoidance. Eucalypts are highly susceptible to *P. psidii* at physiological growth stage A (0 to 2 years old). They are less frequently attacked at stage B (2 to 4 years old) and rarely at stage C (4 years to harvesting; 22). Older plantations, therefore, have very low levels of rust. Environmental conditions also may not be ideal for infection to occur on the actively growing tissue in taller trees. Coppice growth also has been found to be extremely susceptible to *P. psidii* (21). Therefore, it is recommended that trees are not felled when environmental conditions are ideal for infection to occur (46). Also, cuttings should be harvested only from clonal hedges under conditions that do not favor infection by *P. psidii* (46). Alternatively, fungicides can be used to protect the young shoots in this situation (1,2).

Use of resistant genotypes. There is considerable genetic variability within and between *Eucalyptus* spp., and infection studies have shown clear differences in their susceptibility to *P. psidii* (11,17-19,23). From most- to least-susceptible, they include: *E. cloeziana*, *E. phaeotricha*, *E. grandis*, *E. citriodora*, *E. camaldulensis*, *E. tereticornis*, *E. urophylla*, *E. maculata*, *E. paniculata*, *E. punctata*, *E. pycnantha*, *E. microcorys*, *E. pellita*, and *E. saligna*. It has been recommended that the most susceptible species not be planted in countries where the fungus is known to occur. In field trials after a severe attack by *P. psidii*, individual trees of some *Eucalyptus* spp. have been selected that appear resistant (23). Potentially, these can be vegetatively propagated for clonal plantings.

Many *Eucalyptus* spp. from specific provenances have been tested for their

susceptibility to *P. psidii* (11,17,23). Parameters used to quantify resistance of *Eucalyptus* spp. to *P. psidii* include the ratio of diseased to healthy leaves and twigs, and the number and size of pustules (12,17) and uredinia (7,46,47). The latent and generation periods also have been used (37). Trees in plantations have been visually rated using a 0 to 3 scale, where 0 = healthy, 1 = resistant, 2 = moderately susceptible, and 3 = susceptible (21).

Wide-scale plantings of *E. grandis* seed from South Africa led to severe outbreaks of eucalyptus rust in Brazil between 1973 and 1978, and it has subsequently become one of the most serious diseases in that country (20,21,31). The susceptible seedlots were reported to be provenances of *E. grandis* (18). However, the *E. grandis* sent to Brazil from South Africa in the 1970s (N. Denison, Mondi Forests, personal communication) were commercial seedlots and not provenances, as has been reported in the literature.

Fungicides. Fungicides can be successfully employed for disease control in eucalypt nurseries and on coppice (2,3,39,41,44,48). Among the protectant fungicides tested, mancozeb was the most effective against the pathogen when applied 10 days prior to infection. The systemic fungicides triadimenol, triforin, oxycarboxin, and diniconazole were found to be translocated in young tissue and were reported to prevent infection successfully (2,17,44).

International Importance

P. psidii is an unusual rust in that it has an extremely wide host range amongst genera and species of Myrtaceae. Its occurrence on *Eucalyptus* spp. appears to be one of the unexpected and unfortunate consequences of exposing the rust to this host in a non-native situation. The occurrence of *P. psidii* on *Callistemon speciosus*, another Australian myrtaceous plant, in South America, is an example of the same phenomenon. At this stage it would appear that a race or races of the rust are well established on *Eucalyptus* spp. The potential for these fungi to result in epidemic disease situations in the areas of origin of *Eucalyptus* spp., and perhaps other myrtaceous genera, seems real, and could be a serious threat to global biodiversity. Such a situation would be equivalent to other introduced epidemic tree diseases, such as Dutch elm disease (caused by *Ophiostoma ulmi* (Buisman) Nannf. and *O. novo-ulmi* Brasier), chestnut blight (caused by *Cryphonectria parasitica* Murrill (Barr)), pine wilt (caused by *Bursaphelenchus xylophilus* Steiner & Buhner), and white pine blister rust (caused by *Cronartium ribicola* J.C. Fisch).

The three occurrences of rust on *Eucalyptus* spp. outside South and Central America are enigmatic. In all three cases (South Africa, Taiwan, and India), the rusts have been typified only by the uredinial

states, and definitive species identifications have not been made. Only in the case of Taiwan was the rust identified as *P. psidii* (56). Wingfield (unpublished data) also conducted morphological comparisons, including scanning electron microscopy, of the rusts from Taiwan and Brazil and could find no differences between them. Indeed, if the rust in Taiwan is the same as that occurring in Brazil, it is possible that it has been introduced from South or Central America. Given the proximity of Taiwan to Australia, the threat of introduction to eucalypts in their native range would appear to be even more severe.

The wide host range of *P. psidii* makes it a tree pathogen of considerable global importance. Despite this fact, it has not received particularly great attention other than in Brazil, where it causes serious damage to a number of commercial crops. Many, if not most, forest pathologists in the international arena are unaware of this important pathogen, or at least are oblivious to its importance. It is hoped that this review will highlight its significance and possibly even lead to an international effort to evaluate the potential threat associated with it.

Conclusions

P. psidii is considered to be one of the most serious threats to *Eucalyptus* spp. in the world today. Strict quarantine measures are necessary to prevent the entry of this fungus into countries where it does not occur, particularly in Australia, where *Eucalyptus* spp. are native and where epidemic losses could potentially be experienced. Foresters, pathologists, and mycologists involved in quarantine measures should, therefore, be aware of the characteristics of this rust fungus and symptoms associated with infection.

A detailed taxonomic study is needed to determine the host range and geographical distribution of *P. psidii*. It still is not certain whether more than one species of *Puccinia* is capable of infecting members of the Myrtaceae. Comparisons at the molecular level would be particularly useful in this regard.

In order to successfully implement a breeding program, the races of *P. psidii* must be identified. In this respect, comprehensive studies should be undertaken to determine which races are present, the host range of these races, and which race or races are predominant in different regions.

Uncertainty exists on aspects of the life cycle and infection process of *P. psidii*. Modern technology, including electron microscopy and molecular genetic comparisons, will provide researchers with an understanding of the etiology of the disease as well as the behavior of the fungus on incompatible tissue.

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