FULL PAPER

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On some rust fungi (Uredinales) collected in an *Acacia koa–Metrosideros* polymorpha woodland, Mauna Loa Road, Big Island, Hawaii

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Abstract Nine species of rust fungi (Uredinales) were found during a 1-day field study in an Acacia koa-Metrosideros polymorpha woodland in Volcanoes National Park on Big Island, Hawaii. Two species, both found on Acacia koa, are native (endemic) rusts whereas 7 species are nonnative on nonnative hosts, highlighting the high proportion of introduced species in the Hawaiian flora even in more or less natural habitats. One species, Uromyces linearis on Panicum repens, constitutes the first record of this rust for the Hawaiian archipelago, bringing the total to 93 species on the islands, 70 (75.3%) of which are introduced. The species records are annotated with emphasis on the geographic origin of each taxon. In addition, the study has led to the molecular reevaluation of the genus Racospermyces, indicating that it is synonymous with *Endoraecium*, and six new combinations are proposed for the species previously placed in Racospermyces. The high number of introduced species in Hawaii coupled with the paucity of native species when compared to other global regions is discussed.

Key words Ecology · *Endoraecium* · Introduced species · *Racospermyces* · Taxonomy

Introduction

The Hawaiian archipelago, the most isolated island group of comparable size and topographical diversity on Earth, is about 4000 km from the nearest continent (North America). The youngest and largest of the eight major islands, Big Island, covers an area of more than 10455 km² (63% of the

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total area of the state of Hawaii) and exhibits a range of climatic diversity from tropical continuously wet to periglacial (Price 1973). This long period of evolutionary isolation has resulted in many endemic species in Hawaii. For example, the native flowering plant flora totals about 956 species, of which approximately 850 are endemics (Wagner et al. 1990). But today, as is true for all other oceanic islands, this long period of isolation has left the Hawaiian Islands vulnerable to human impact and nonnative biota that may threaten natural ecosystems and replace native biota (Loope and Müller-Dombois 1989). The rate of introduced species immigration began to rise upon the arrival of the Polynesians in the fourth century A.D. and was greatly accelerated after James Cook's arrival in Hawaii in 1778 (Nagata 1985). Today there are more introduced plants in the Hawaiian Archipelago than native ones. Yee and Gagné (1992) documented more than 8000 introduced species or cultivars, 861 of which are established aliens. At least 149 species are weeds of natural areas alone (Motooka et al. 2003).

In contrast to many animal groups and vascular plants that have been studied, studies on the diversity and distribution of Hawaii's fungi are scarce. One group, the rust fungi (Uredinales), has been documented more intensely than most. The first list of rust fungi of Hawaii was published by Stevens (1925), who reported 39 species. In the subsequent decades, various authors have added to the species records for the Hawaiian Islands; the majority of these newly recorded species, however, are suspected of being introduced. In 2005, the authors and three additional mycologists (Lisa Castlebury, USA; Sarah Hambleton, Canada; and Shaun Pennycook, New Zealand) had the opportunity to collect rust fungi in a more or less natural forest area in Hawaii's Volcanoes National Park. In this article, we report on nine rust species found along the Mauna Loa Road at approximately 1000 m elevation. These species are described, annotated, and discussed with particular emphasis on the origin of introduced species. In addition, this study has led to the molecular reevaluation of the genus Endoraecium Hodges & D.E. Gardner and Racospermyces J. Walker, and six new combinations are proposed.

Observation area

Field studies were carried out on August 5, 2005, along the Mauna Loa Road, Hawaii Volcanoes National Park, E. Mauna Loa, Kilauea Caldera, 500-1500 mN of Highway 11 on the Big Island of Hawaii. Coordinates for the general collecting locale are 19° 26.281'N 155° 18.334'W, about 900-1200 m. The area has a temperate climate characterized by warm summers and adequate precipitation in all months (Price 1973). Mauna Loa Road is a narrow road mainly used by hikers, composed of lava soil. This midelevation mixed mesic forest is characterized by two endemic trees, koa (Acacia koa A. Gray, Fabaceae) (Fig. 1) and ohi'a-lehua (Metrosideros polymorpha Gaudich., Myrtaceae) (Fig. 2). In contrast, the herbal plant flora is dominated by introduced plants, particularly along the side of the road, evidencing the human impact on the ecosystem. Among these, exotic Poaceae species are very common.

Material and methods

Rust fungi were collected on August 5, 2005, and dried in a standard plant press. Dried material was examined in tap water mounts by light microscopy (Zeiss Axioskop 2 Plus). Pertinent features were measured at a magnification of 400 or 1000×. For spore measurements, 25 spores were evaluated. Host plants were identified by the authors and H. Scholz (Poaceae); Uredinales were collected by the participants and identifications were confirmed by M. Scholler or M.C. Aime (*Kuehneola uredinis*) with the aid of various literature (McAlpine 1906; Arthur 1934; Cummins 1971; Hodges and Gardner 1984; Walker 2001). Spore state nomenclature follows Cummins and Hiratsuka (2003). Specimens studied are deposited in KR, with duplicates in BPI.

Methods for DNA extraction, amplification, sequencing, and analyses are detailed in Aime (2006). Taxa were selected for analyses to include (1) exemplars from each genus placed in the Pileolariaceae into which Endoraecium and Racospermyces are traditionally classified (Cummins and Hiratsuka 2003); (2) exemplars from the genus Ravenelia Berk., to which prior phylogenetic analyses suggest Endoraecium is allied (Aime 2006); (3) outgroups from nonuredinalian Urediniomycetes. New sequences have been deposited in GenBank, DQ323916-323926; voucher material from which new sequences were derived is deposited in BPI (U.S. National Fungus Collections, Beltsville, MD, USA) or BRIP (National Collection of Fungi, Queensland, Australia). Sequences from two nuclear rDNA regions [28S large subunit (LSU) and 18S small subunit (SSU)] were assembled for the following: Pileolaria brevipes Berk. & Ravenel (LSU: on Toxicodendron sp., Clearwater, MN, USA, September 05, 2004, coll. & detr. Bob Stack s.n., BPI 871761, GenBank = DQ323924); Pileolaria brevipes (SSU: GenBank #AY123314); Uromycladium tepperianum (Sacc.) McAlpine (on Acacia saligna (Labill.) H.L. Wendl., Western Cape, South Africa, October 12, 2004, coll. & detr. Alan Wood s.n., BPI 871523, GenBank LSU = DQ323922, SSU = DQ323923); Uromycladium tepperianum (SSU: GenBank #AY125418); Uromycladium fusisporum (Cooke & Massee) Savile (on Acacia salicina Lindl., QLD, Australia, December 13, 2000, coll. & detr. R. Shivas, BRIP 27608, GenBank LSU = DQ323921); Uromycladium notabile (Ludw.) McAlpine (SSU: GenBank #AY125416); Ravenelia echinata var. ectypa (Arthur & Holw.) Cummins (on Calliandra formosa (Kunth) Benth., Tucuman, Argentina, April 2, 1994, coll. J. Hennen ARG94-073, detr. J. Hernandez, BPI 841034, LSU = DQ323925); Ravenelia macrocarpa Syd. & P. Syd. (on Senna subulata (Griseb.) H.S. Irwin & Barneby, Catamarca, Argentina, September 24, 1997, coll. J. Hennen ARG97-056, detr. J. Hernandez, BPI 841195, LSU = DQ323926); Endoraecium acaciae Hodges & D.E. Gardner





Fig. 1. Old *Acacia koa* population on Mauna Loa Road. (photograph, M.C. Aime)

Fig. 2. Metrosideros polymorpha vegetation on Mauna Loa Road. (photograph, M. Scholler)

(on Acacia koa, Big Island, Hawaii, USA, August 5, 2005, coll. D. & E. Farr, detr. M.C. Aime MCA2957, BPI 871098, LSU = DQ323916, SSU = DQ323917); Racospermyces koae (Arthur) J. Walker (on Acacia koa, Big Island, Hawaii, USA, August 5, 2005, coll. & detr. M. Scholler & M.C. Aime MCA2961, BPI 871071, LSU = DQ323918, SSU = DQ323919); Racospermyces koae (SSU: GenBank #AY125387); Endoraecium hawaiiense Hodges & D.E. Gardner (on Acacia koa, Big Island, Hawaii, USA, August 5, 2005, coll. & detr. M. Scholler & M.C. Aime MCA2962, BPI 871064, LSU = DQ323920); Racospermyces digitatus (G. Winter) J. Walker (SSU: GenBank #AY125400); Eocronartium muscicola (Pers.) Fitzp. (LSU: GenBank #AY512844; SSU: GenBank #AY123323); Platygloea vestita Bourdot & Galzin (LSU: GenBank #AY512872; SSU: GenBank #AY124480).

Results

Annotated list of species

Kuehneola uredinis (Link) Arthur, 0,I on Rubus argutus Link (Rosaceae), epiphyllous on leaves, infected with hyperparasitic Tuberculina sp., ~900m (BPI 871065). Kuehneola uredinis has an almost worldwide distribution (Gäumann 1959) but is introduced in Hawaii. It has been reported to cause minor infection on two endemic Hawaiian Rubus species, R. hawaiensis A. Gray and R. macraei A. Gray (Gardner and Hodges 1989). Reports of K. uredinis on R. villosus in Hawaii (Stevens 1925) should be referred to R. argutus (Gardner and Hodges 1989). Rubus argutus is native to the eastern and central United States and is an aggressive pest in parts of Hawaii. According to Gardner (1998), the rust may have been introduced with the introduction of R. argutus.

Phakopsora tecta H.S. Jacks. & Holw., II on Commelina diffusa Burm. f. (Commelinaceae), ~900 m (KR 0013972; BPI 871066). The host is native to the Old World tropics but is widely naturalized in Hawaii whereas the rust is probably a native of the Neotropics (with the type locality in Bolivia). Almost every individual plant was infected, confirming Gardner's (1981, 1998) observation that it "is consistently present wherever the host occurs." No telia were observed (Fig. 3).

Puccinia cnici G. Martin, II, III on Cirsium vulgare (Savi) Ten. (Asteraceae), ~1000 m (KR 0013976; BPI 871067). This introduced rust is naturally distributed in the Northern Hemisphere (Gäumann 1959). The host is a native of Eurasia. Gardner (1997) recorded the rust species for the first time in Hawaii but did not provide information about record localities and dates.

Puccinia coronata Corda, III on Holcus lanatus L. (Poaceae), ~1000 m (KR 0013974; BPI 871068). Puccinia coronata is a heteroecious species complex on Rhamnaceae (aecial hosts) and Poaceae (telial hosts) with circumglobal distribution according to Cummins (1971). Puccinia coronata only infects introduced grass species in Hawaii,

occurring on *H. lanatus* (native of Europe, temperate Asia, North Africa), and on *Hordeum vulgare* L. of Middle Eastern origin (Gardner and Hodges 1989). Similar to *P. poae-nemoralis*, *P. coronata* persists in Hawaii without the aecial host.

Puccinia leveillei Mont., III on Geranium spec. (Geraniaceae), ~900 m (KR 0013971; BPI 871069). Puccinia leveillei (= P. geranii-sylvatici P. Karst.) is also known from North and South America, Europe, and Asia (Gäumann 1959). In Hawaii, it has been found previously only on the endemic shrub Geranium cuneatum Hook. (Gardner 1994). All herbaceous Geranium spp. are naturalized aliens in Hawaii (Wagner et al. 1990: 728). Geranium spec. is herbaceous. Consequently, it is introduced as well although we couldn't contic it to a certain species. Because of its occurrence on a native host only, Gardner (1994) considered this rust an indigenous one. The nonnative origin of the new host and the general nordic-alpine distribution of the rust, however, do not support this assumption. Figure 4 shows the conspicuous telia on petioles.

Puccinia poae-nemoralis G.H. Otth (P. brachypodii var. poae-nemoralis (G.H. Otth) Cummins & H.C. Greene), II on Anthoxanthum odoratum L. (Poaceae), ~1000 m (KR 0013973; BPI 871070). At present, this heteroecious species has a circumglobal distribution in temperate regions and higher altitudes of the tropics (Cummins 1971), but its origin is probably in Europe and Asia. Besides A. odoratum, the species has been recorded on the Hawaiian Islands on Poa annua and P. pratensis (Gardner and Hodges 1989). All three host plants are natives of Eurasia. Gardner and Hodges (l.c.) remark that no voucher specimen existed for a former record of this rust on A. odoratum. On Hawaii, P. poae-nemoralis persists without the aecial host (Berberis spp., Berberidaceae).

Uromyces linearis Berk. & Broome, II, III on Panicum repens L. (Poaceae), ~1000m (KR 0013975: BPI 871072). Uredinia small, linear, on adaxial leaf surface, aparaphysate; urediniospores 24.0–28.0 × 22.0–25.0 μm, globoid, wall 2-3 µm, densely and irregularly echinulate, pores 4-5, almost equatorial, rarely scattered. Telia on adaxial leaf surface, small, linear, compact, black; teliospores $21.0-27.5 \times 18.5-22.5 \mu m$, typically obovoid, wall smooth, up to 2.5 μm at side, up to 7 μm at apex, germ pore without papilla, pedicels yellowish, thick walled, up 65 µm long and 13.5 µm wide. Telia partly overgrown by the mold Epicoccum purpurascens Ehrenb. Uromyces linearis is a newly introduced species for the Hawaiian Islands. Thus far the species has been recorded from Africa, the Mediterranean, and Eastern Asia to Japan (Hiratsuka et al. 1992); it is known only from its type host, Panicum repens (Cummins 1971). The plant is an introduced invasive in Hawaii of probable Asian origin.

Endoraecium hawaiiense Hodges & D.E. Gardner, 0, II^{III} on Acacia koa (Fabaceae), ~1100 m (KR 0013978; BPI 871064). This is one of two endemic species we found and a first record for Big Island. Previously this species was found rarely at a few sites on Oahu only (Gardner 1994). The species causes conspicuous witches' brooms on older trees (Fig. 6). Although telia were formed all over the surface of

phyllodes, black pycnia were found mainly on the tips of heavily deformed phyllodes. No germ tubes as described by Hodges and Gardner (1984) could be observed in the dried material.

Racospermyces koae (Arthur) J. Walker, I, III on Acacia koa (Fabaceae), ~1100 m (KR 0013977; BPI 871071). This is the second endemic species we found on Mauna Loa Road. No pycnia were observed. Aeciospores and teliospores were formed in the same sorus. Sori 3–4 mm, mainly on phyllodes (Fig. 5), but we observed sori also on leaflets and shoots, causing minor deformations, but no witches' brooms. The fungus was only found on young trees.

Prior molecular analyses of two nuclear rDNA gene regions (LSU and SSU) suggested that *Endoraecium* and *Racospermyces* are congeneric (Aime 2006). In the present study, additional sequence data were obtained and compared for several species of *Endoraecium* and *Racospermyces*, including the type species of each genus, *E. acaciae* Hodges & D.E. Gardner and *R. digitatus* (G. Winter) J. Walker (Fig. 7). Although statistical support for

some recovered nodes is low because of missing data in the two-gene analyses, results confirm that *Endoraecium* and *Racospermyces* are congeneric (Fig. 7).

For the species of Atelocauda Arthur & Cummins (Pileolariaceae) with reticulate urediniospore walls, type 5 as opposed to type 7 spermogonia/pycnia (Hiratsuka and Hiratsuka 1980), and hosts confined to the Mimosoideae (Fabaceae), Walker (2001) described a new genus, Racospermyces, containing six species. Racospermyces koae is one of five closely related species in Hawaii on the endemic host Acacia koa. All five species are native and four are endemic to Hawaii. Three species in the Hawaiian complex are currently placed in *Racospermyces*. The other two, both endemic, are placed in the genus *Endoraecium*; these can be considered endocyclic variants of the species placed in Racospermyces - in addition to forming pycnia, they form spores that morphologically resemble typical urediniospores but germinate with a basidium-like germ tube (Hodges and Gardner 1984), i.e., functionally a teliospore (fide Cummins and Hiratsuka 2003). Given that



Fig. 3. Commelina diffusa strongly infected by Phakopsora tecta. (photograph, L. Castlebury)

Fig. 4. Puccinia leveillei on leaf sheaths and petioles of Geranium homeanum, a plant native of Australia

Fig. 4. Puccinia leveillei on leaf sheaths and petioles of Geranium homeanum, a plant native of Australia and New Zealand. (photograph, M. Scholler)

Fig. 5. Endoraecium koae (Racospermyces koae), an endemic species forming sori on phyllodes of young Acacia koa trees. (photograph, M. Scholler)

Fig. 6. Endoraecium hawaiiense, an endemic species forming small witches' brooms on Acacia koa. (photograph, M. Scholler)

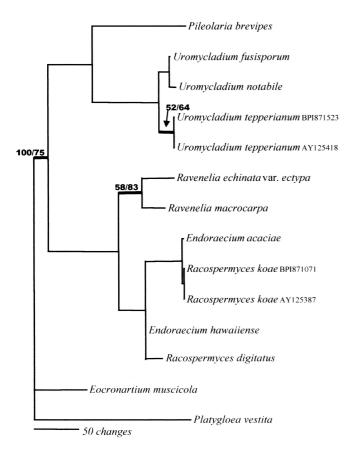


Fig. 7. One of six most parsimonious (MP) trees resulting from combined nuclear 28S and 18S rDNA analyses. The same topology was achieved with maximum-likelihood (ML) analyses produced by the quartet puzzling method. *Thickened branches* indicate nodes statistically supported by both methods (i.e., by bootstrap replicates for MP and quartet puzzling reliability values); numbers above branches are bootstrapping/quartet puzzling values

it has long been assumed that endocyclic forms are typically derived from aecial states of longer-cycled rusts (Laundon 1974; Buriticá and Hennen 1980), the delimitation of genera based solely on life-cycle variants is no longer tenable. Based on the close similarities in aeciospore and urediniospore morphology, host preference, and similarities in life cycle (Hodges and Gardner 1984; Gardner and Hodges 1985) as well as the molecular results (Fig. 7), we therefore propose reducing *Racospermyces* to synonymy with *Endoraecium* and make the following combinations.

Taxonomy

Endoraecium Hodges & D.E. Gardner, Mycologia 76(2): 339 (1984) emend. M. Scholler & Aime

Typus generis: *Endoraecium acaciae* Hodges & D.E. Gardner, Mycologia 76(2): 339 (1984).

=*Racospermyces* J. Walker, Australasian Mycologist 20(1): 13 (2001).

In a detailed study, Walker (2001) considered *Atelocauda* (currently placed in the Pileolariaceae fide Cummins & Hiratsuka 2003) to be more closely allied to *Dicheirinia* Arthur (Raveneliaceae) than other members of the

Pileolariaceae. The results from this study (Fig. 7) and that of Aime (2006) show that *Endoraecium* is more closely allied to *Ravenelia* (Raveneliaceae) and should also be transferred to that family.

Endoraecium angustiphyllodium (D.E. Gardner) M. Scholler & Aime comb. nov.

Basionym: Atelocauda angustiphyllodia D.E. Gardner [as "angustiphylloda"], Mycologia 83(5): 650 (1991).

Racospermyces angustiphyllodius (D.E. Gardner) J. Walker, Australasian Mycologist 20(1): 21 (2001).

Endoraecium bicinctum (McAlpine) M. Scholler & Aime comb. nov.

Basionym: *Uromyces bicinctus* McAlpine, The Rusts of Australia p. 93 (1906).

Racospermyces bicinctus (McAlpine) J. Walker, Australasian Mycologist 20(1): 16 (2001), and synonyms therein.

Endoraecium digitatum (G. Winter) M. Scholler & Aime comb. nov.

Basionym: *Uromyces digitatus* G. Winter, Revue de Mycol., Toulouse 8: 209 (1886).

Racospermyces digitatus (G. Winter) J. Walker, Australasian Mycologist 20(1): 13 (2001), and synonyms therein.

Endoraecium hyalosporum (Sawada) M. Scholler & Aime comb. nov.

Basionym: *Uromyces hyalosporus* Sawada, The Botanical Magazine (Tokyo) 27 (No. 313-324): 19 (1913).

Racospermyces hyalosporus (Sawada) J. Walker, Australasian Mycologist 20(1): 17 (2001), and synonyms therein.

Endoraecium koae (Arthur) M. Scholler & Aime comb. nov.

Basionym: *Uromyces koae* Arthur, in Stevens, Bernice P. Bishop Museum Bulletin 19: 118 (1925).

Racospermyces koae (Arthur) J. Walker, Australasian Mycologist 20(1): 20 (2001), and synonyms therein.

Endoraecium tierneyi (J. Walker & R.G. Shivas) M. Scholler & Aime comb. nov.

Basionym: *Racospermyces tierneyi* J. Walker & R.G. Shivas, in Walker, Australasian Mycologist 20(1): 23 (2001).

Discussion

Nine species of Uredinales were found along the Mauna Loa Road, two of which are native (endemic) and seven of which are introduced established aliens, i.e., neomycetes (Kreisel and Scholler 1994), on nonnative naturalized plants. One of the neomycetes (*Uromyces linearis*) was found for the first time in the Hawaiian Archipelago. The origin of the introduced fungi (and many other introduced species known from Hawaii) indicates that species have been introduced from all continents. Furthermore, this study shows that even more or less natural habitats such as the *Acacia koa-Metrosideros polymorpha* woodlands in the Volcanoes National Park are dominated by alien species.

Table 1. The number of rust fungi relative to the number of native plants in northeast Germany (Pomeranian Boddenlandscape), the Hawaiian archipelago, and New Zealand

| | NE Germany | Hawaii | New Zealand |
|--|----------------------|------------------|-------------------|
| Area (km²) Number of native rust species Number of introduced rust species Number of native vascular plants Quotient native rusts/native vascular plants | 4620 | 10 455 | 268 680 |
| | 179 ^a | 23° | 104°.g |
| | 10 ^a | 70° | 127°.g |
| | c. 1090 ^b | 956 ^d | 2066 ^f |
| | 0.16 | 0.02 | 0.05 |

^a Scholler (1996)

Based on the recent publications by Gardner (1994, 1997) and Gardner and Flynn (1998), we calculated that on the Hawaiian Islands there are a recorded 92 rust species. After reclassifying *Puccinia leveillei* as nonnative (see above), there are only 23 native species, with 19 of these being endemic. The presence of a newly recorded species (*U. linearis*) brings the total number of species to 93, and the number of introduced species to 70, i.e., more than 75% of the known Uredinales flora.

Recently, changes in the rust flora have been documented in detail in a Northern Hemisphere temperate region, namely in the Pomeranian Boddenlandscape in NE Germany (Scholler 1996) and in the New Zealand archipelago (McKenzie 1998). A comparison of the two rust floras with the Hawaiian one with respect to diversity and origin of species is quite interesting (see Table 1). The total number of native rust species and the number of native rust species relative to the number of potential native hosts (vascular plants) is highest in NE Germany and lowest in Hawaii. As conjectured by Stevens (1925), who studied fungi for 5 months in Hawaii in 1921, this paucity of indigenous rust species is thought to be one effect of the remoteness of Hawaii from sources of colonization rather than being caused by any intrinsic unfavorable conditions for their development. On the other hand, the relative number of introduced species is highest in Hawaii, followed by New Zealand. Within New Zealand, however, there is a strong contrast between the distribution of rusts in the almost subtropical north and in the temperate South Island. Native fungus species dominate in the south, and the north is richer in both the number of introduced species and the total number of species.

In NE Germany, a 4-year field study on the changing rust flora revealed an increase of 10 species but a loss of 46 species, resulting in a negative balance (Scholler 1996). Corresponding studies have not been carried out elsewhere, but McKenzie (1998: 239) for New Zealand as well as Gardner (1994: 977) for Hawaii indicate that there are several species with very local distributions and narrow host ranges that have not been rediscovered for decades, and thus may now be extinct. Nevertheless, the absolute number of new species in New Zealand and in Hawaii is by far

higher than the number of extinct ones, and overall there has been an increase in species numbers for both. This local increase in species richness owing to the presence of invaders is generally at the expense of decreased differentiation among regions and has been termed biotic homogenization (Vitousek et al. 1997). During the process of biotic homogenization, biological communities on the worldwide scale become increasingly similar, as certain introduced species become highly successful. Others decline and face extinction (McKinney and Lockwood 1999).

Multiple factors may contribute to this increase in rust species numbers, but the similarity between Hawaii and New Zealand (the north in particular) is obvious and may have common causes. According to Simberloff (1995), certain ecological groups are missing in the Pacific Islands, which makes the islands particularly susceptible for (rustinfected) invasive plants. Also, warmer climates seem to provide more favorable conditions for the introduction of plants and their rusts. Plants are often crop and ornamental plants of tropical or subtropical origin that find ideal conditions in warmer climates. Other factors may be important as well, such as increasing international traffic through mass tourism, military bases, etc., although this is of concern for NE Germany as well. A special problem for New Zealand are airflows that may transport rust spores over long distances from Australia (McKenzie 1998).

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^bBenkert et al. 1996

^cScholler and Aime (2006, this publication)

^d Wagner et al. (1990)

^e McKenzie (1998); Wilton and Breitwieser (2000; seed plants); Large and Braggins (1991; ferns)

^gThree additional species listed by McKenzie (l.c.) with unknown origin were not considered for this calculation

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