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FULL PAPER

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Life cycle and life strategy features of *Puccinia glechomatis* (Uredinales) favorable for extending the natural range of distribution

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Abstract The objective of this study was to find features in microcyclic rust fungi (Uredinales) on wild host plants favorable for extension of the natural range of distribution. *Puccinia glechomatis*, a leptosporic rust fungus and its herbal host *Glechoma hederacea* (Lamiaceae), both natives to Eurasia and introduced in North America, were used for this study. Although the host has been known from North America since the beginning of the nineteenth century, the rust fungus was first observed there only in recent years. Favorable features were identified by studying the life cycle of the rust, including nuclear conditions and seasonal characteristics as well as its spread in North America. The life cycle was studied macroscopically by inoculation experiments, by various light microscope techniques, and by scanning electron microscopy. The spread of the pathogen and its host were reconstructed by evaluating host plant herbarium specimens and databases, literature, and field study data. The studies on *P. glechomatis* show that, generally for microcyclic rust fungi, establishment and potential for spread are based on several favorable features of both the host (e.g., synanthropic occurence and dispersal, genetic stability, regeneration of vegetative plant parts) and the rust fungus (asexual reproduction/genetic stability, homothallism, propagation with host plant, formation of both leptospores and thick-walled teliospores).

Key words *Glechoma hederacea* · Herbaria · Invasive species · *Puccinia lagenophorae* · Neomycete · North America

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Introduction

Rust fungi (Uredinales) are obligate biotrophic plant parasites, which typically cause only minor damage to a population of wild host plants in an area belonging to their natural range of distribution. Introduced plant parasites and established alien fungi (named neomycetes by Kreisel and Scholler 1994), however, may cause severe damage and even mortality, especially on non-resistant host individuals such as genetically uniform monocultures of forest trees, crops, and ornamental plants. The introduction, spread, and epidemiology of some of these economically important rust species are well documented, e.g., the white pine blister rust *Cronartium ribicola* J. C. Fisch. (Gäumann 1951) and the southern maize rust *Puccinia polysora* Underw. (Gregory 1973). On the other hand, little is known about spreading rust neomycetes on wild (natural or naturalized) host plants and their strategies. Recently, Scholler (2000) found a microcyclic species, *Puccinia glechomatis* DC., for the first time in North America (records from New York in 1998 and Indiana in 1999). The rust is native to Eurasia from western Europe to Siberia and Japan and from the Mediterranean to Scandinavia (Sydow and Sydow 1904). The fungus is autoecious and microcyclic, forming telia and basidia (Fig. 1). Teliospores may germinate immediately without a resting period (lepto-form). The fungus is restricted to Lamiaceae species of the genus *Glechoma* L. and to *Meehania urticifolia* Makino (=*Dracocephalum urticaefolium* Miq.) (see Gäumann 1951; Hiratsuka et al. 1992; Zhuang 2003). The most common host species is *Glechoma hederacea* L. (ground-ivy), which is native to Eurasia as well. Its invasion history in North America has been documented recently (Böllmann and Scholler 2004). The plant was first reported in 1806 on the East Coast of North America and spread mainly westward, with an estimated average speed of 30 km per year. On the West Coast, it was first found in 1893. The perennial plant is common in manmade habitats and spreads over short distances primarily asexually (clonally) by trailing stems (stolons) (Hutchings and Price 1999). Over longer distances, the

plant is dispersed by vegetative fragments (Uva et al. 1997).

In the following we provide a study on the life cycle of *P. glechomatis* and its invasion in North America to find and discuss special features favorable for microcyclic rust fungi on wild host plants to expand their natural range of distribution. Some general rules for successful microcyclic rust neomycetes are postulated.

Material and methods

Life-cycle studies

For inoculation experiments, rust-infected and uninfected *Glechoma hederacea* plants were collected at various sites in Indiana (United States). All plants were cultivated in the greenhouse in 15-cm-diameter pots containing topsoil mixed with peat moss under natural light conditions at 20° ± 2°C during the daytime and 18° ± 2°C at night and were fertilized (All Purpose Plant Food, Sam's Choice) occasionally according to the label.

Inoculation experiments were carried out in the greenhouse or in petri dishes. To inoculate leaves and agar, leaf parts with telia were pasted inside a petri dish lid (Narisawa et al. 1993; Crane et al. 2000b) with 1.5% water agar and were either elevated 20–30 cm over potted plants to obtain a better distribution of the basidiospores or positioned over leaves and agar in a petri dish. Relatively high humidity was maintained by covering the potted plants and the elevated telia with a plastic bag, and by moist filter paper or agar within the petri dishes, which were sealed with parafilm. Plants in the greenhouse were inoculated at 6 PM and incubated for 15 or 40 h. To monitor the amount of inoculum produced, one 18-mm^2 cover slip per pot was placed on or next to the leaves, and the collected basidiospores were counted under a light microscope at 200× (Crane et al. 2000a,b). Leaves in petri dishes and water agar plates were inoculated in darkness at 20°C for 6–15 h. After exchanging the lid, plates were kept under these conditions until examination or were incubated in a growth chamber (VWR Scientific Products) at 20°C and a 12-h photoperiod.

For germination studies, teliospores were suspended in aqueous 0.05% (v/v) Tween 20 and transferred to 1.5% water agar plates, to glass slides, to plastic petri dishes, or directly from the leaf onto a water droplet on a glass slide (Gardner 1981), which was placed in a moist petri dish. All treatments were incubated at 20°C in darkness up to 48 h. The germination was also tested at 10° and 6°C.

For light microscopy, the following microscopes and accessories were used: a Nikon Optiphot compound microscope and a Nikon Diaphot inverted microscope, both with an epifluorescence attachment with a 100 W high-pressure mercury lamp and UV block filter, and a Nikon SMZ-10 dissecting microscope and Nikon FX-35A camera using Kodak Ectachrome 160 T slide film with a Nikon UFX exposure control. Nuclei at all stages were stained with the fluorocrome DAPI (4,6-diamino-2-phenylindole; Sigma) according to Gardner (1996) and Crane et al. (2000a,b) for 10–60 min. Either a 1 µM or a 10 µM DAPI solution was prepared in McIlvaine's buffer (one part 0.1 M citric acid: four parts 0.2 M Na_2HPO_4, pH 7.0). The 1 µM preparation was sufficient for basidiospores, but a 10 µM preparation gave better results with teliospores. To study spores and mycelium at all stages, material of all treatments was stained with methylene blue for 5–10 min and rinsed twice or mounted immediately in 0.05% Tween 20 solution on a glass slide with a cover glass.

Teliospores and basidiospores on agar were initially observed directly in the closed petri dish with the inverted microscope to avoid desiccation of the spores. Preselected areas of agar were cut out and mounted for observation with the compound microscope. To study germination and penetration of basidiospores on a leaf surface, young inoculated leaves were stained and mounted immediately or were first processed to obtain adaxial epidermal tissue. To study the formation of mycelium and teliospores, intact leaf sections with telia were mounted directly on a slide as described above, or the lower epidermis with cells of the spongy mesophyll adjacent to telia were removed while the leaf was submerged in 0.005% Tween 20 solution. Leaf cross sections through and adjacent to telia were prepared manually with a razor blade.

To study the overwintering strategies of *P. glechomatis*, teliospores of several herbarium specimens from North America and Europe from two herbaria (PUR, KR), and freshly collected materials were examined for pigmentation and wall thickness. Three sori formed in the previous year were studied for basidiospore formation from fresh material collected in the following spring (PUR N2640).

For scanning electron microscopy (SEM), fungal structures in or on fresh host tissue were submerged for 2 h in 2% glutaraldehyde buffered in a 0.1 M K_2PO_4 and 0.1 M Na_2PO_4 solution at pH 6.8. After three rinses in the phosphate buffer, samples were submerged in phosphate buffer containing 1% osmium tetroxide for 1 h. Teliospores with basidia were incubated in osmium tetroxide vapor overnight. The material was briefly rinsed in buffer and dehydrated in a series of washes with 30%, 50%, 70%, and up to 100% ethanol and dried in a critical point dryer. The material was mounted with colloidal silver or carbon tape onto metal blocks and coated with gold-palladium in a Hummer 1 sputter coater. Samples were examined with a JEOL JSM-840 scanning electron microscope with digital image acquisition at 5 kV accelerating voltage.

Documention of spread and distribution

Floristic assessments of obligate plant parasitic microfungi have shown that introduced species are generally more abundant after establishment than native species (Scholler 1996, 1999). This occurs because, in their native habitat, plant hosts and their pathogens evolved together; thus, there is generally some host resistance as well as other antagonists that maintain a disease in equilibrium. However, when a fungus is introduced into a new habitat, the

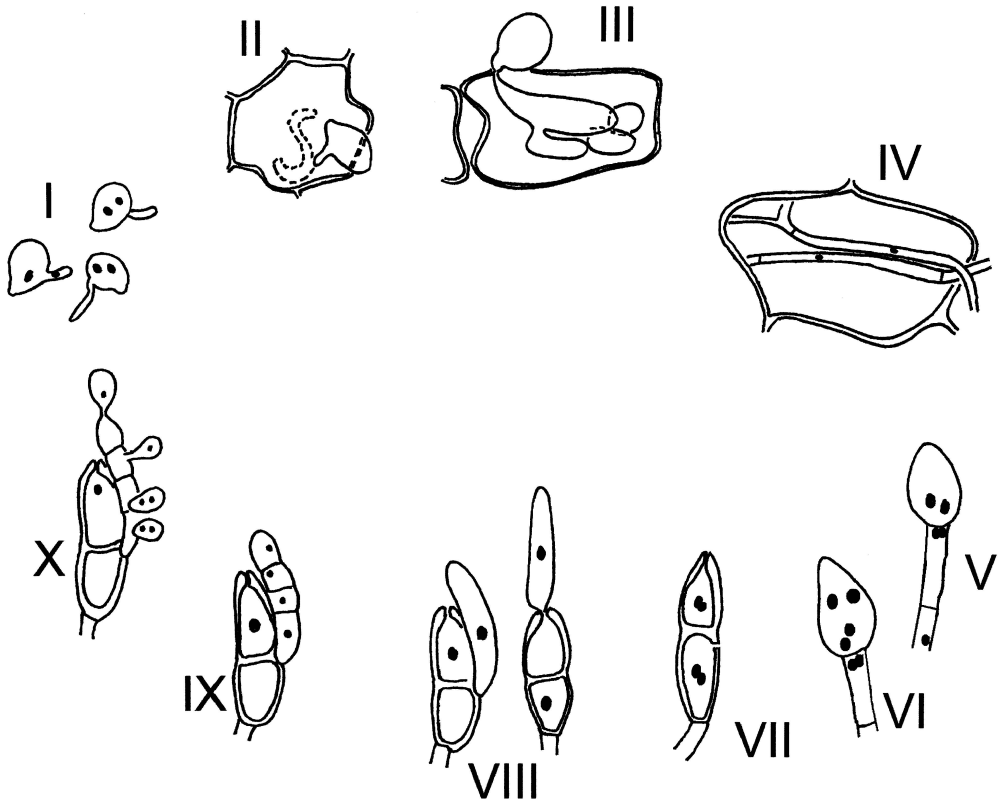

Fig. 1. Life cycle of *Puccinia glechomatis*. **I** Nuclear division and germ tube formation. **II** Apressorium formation on host epidermis and haustorium formation within cell. **III** Apressorium and haustorium formation. **IV** Monocariotic intercellular mycelium. **V** Teliospore formation with binucleate pedicel. **VI** Tetranucleate one-celled teliospore. **VII** Two-celled teliospore, karyogamy. **VIII** Basidium formation. Migrating of fused nucleus. **IX** Mitoses, phragmobasidium formation. **X** Formation of sterigma, basidiospores; migration of nuclei in basidiospores (drawings semischematic)

disease can develop and spread rapidly because of weak resistance and absence of natural antagonists (Palm and Rossmann 2003). Consequently, it is possible that a considerable amount of *P. glechomatis* may have been collected unintentionally with its host plant and incorporated in plant herbaria. Therefore, more than 1400 specimens of *G. hederacea* from North American higher plant herbaria collected in North America after 1970 were examined for rust infections to reconstruct the introduction and spread of the rust. Further data were obtained from field studies. Obtained data were organized in a data bank using the software Filemaker Pro and Excel, maps were created with ArcView, and graphs and pictures were modified using PowerPoint and Adobe Photoshop. The occupied area was measured with the software ASSESS, version 2002. Voucher specimens used for this study collected during field trips or obtained from inoculation experiments were dried and deposited in the Arthur Herbarium (PUR). Also, fragments from specimens of other herbaria (with permission from the given curator) were incorporated in PUR.

Results

Life cycle

Basidiospores were usually binucleate and very rarely (<2%) uni-, tri-, or tetranucleate (Figs. 1-I, 10). Usually, one nucleus remained in the spore and the other one migrated into the germ tube. They germinated on the leaf surface with a small germ tube (Figs. 1-II, 3) and after formation of a small appressorium (Figs. 1, 2), the fungus penetrated an epidermal cell and usually formed haustoria within this cell (Figs. 1-II, 1-III, 5). In some cases, haustoria developed around the nucleus of the host cell (Fig. 6). Attempts to stain the nuclei of the haustorium were not successful. Ten to 13 days after inoculation, telial primordia became visible. The fungus formed a dense monokaryotic intercellular, but very localized, mycelium (Fig. 1-IV) around the initial sorus and secondary sori in a more or less circular pattern. No systemic growth was observed (Fig. 1-IV). No fusion (somatogamy) of hyphae was observed to form a binucleate mycelium. The first binucleate cell before teliospore formation was the cell forming the pedicel of the teliospore (Figs. I-V, I-VI, 8, 10). After another nuclear division, the one-celled developing teliospore became tetranucleate (Fig. 1-VI), and after septation, the typical *Puccinia* teliospore was formed with each cell containing two nuclei that finally fused (karyogamy) (Fig. 1-VII, 8). At 10° and 20°C, but not at 6°C, and high humidity, teliospores germinated without a resting period to form a basidium. The diploid nucleus migrated into the basidium (Figs. 1-VIII, 9), and after meiosis each of the four cells contained one haploid nucleus (Figs. 1-XI, 10, 11). Each cell formed a sterigma (Figs. 1-X, 11) and subsequently a basidiospore. Nuclei of the basidial cells migrated into the developing basidiospore (Fig. 1-I, 10) where they underwent another nuclear division resulting in binucleate basidiospores as previously described. Teliospores showed a tendency for the apical cell to germinate

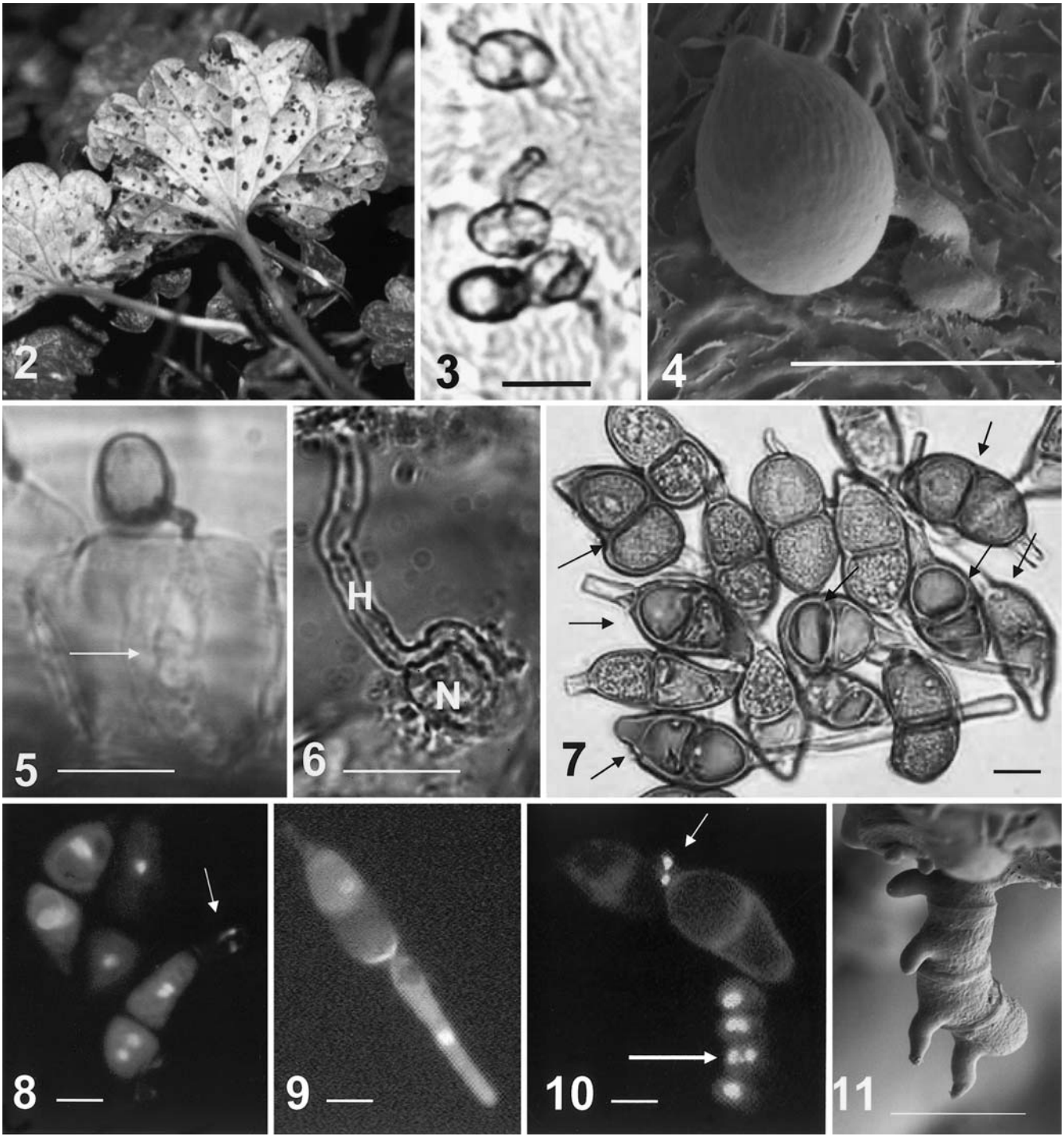

Fig. 2. Telia of *Puccinia glechomatis* on adaxial leaf surface of *Glechoma hederacea*
Fig. 3. Germinating basidiospores on epidermis. *Bar* 10 µm
Fig. 4. Germinating basidiospore with appressorium. *Bar* 10 µm
Fig. 5. Germinating basidiospore with appressorium, and haustorium (*arrow*). *Bar* 10 µm
Fig. 6. Haustorium (*H*) growing around nucleus (*N*). *Bar* 10 µm
Fig. 7. Two types of teliospores: dark thick-walled ones (*arrows*) and pale thin-walled ones. *Bar* 10 µm
Fig. 8. Teliospore cells before, during, and after karyogamy. *Arrow* shows binucleate pedicel cell. *Bar* 10 µm
Fig. 9. Germinating teliospore cell. The nucleus is migrating into the young unicellular basidium. *Bar* 10 µm
Fig. 10. Basidiospores just before and after (*large arrow*) nuclear division to form binucleate spore. *Small arrow*, binucleate pedicel. *Bar* 10 µm
Fig. 11. Four-celled basidium after basidiospore release. *Bar* 10 µm

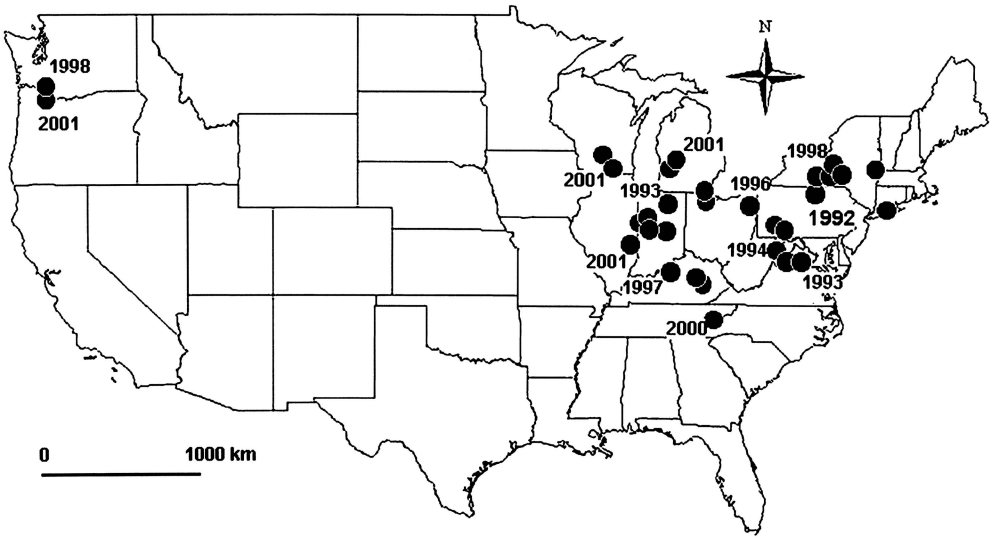

Fig. 12. Records and distribution of *Puccinia glechomatis* in the United States until 2002. The *years* indicate the first record in the pertinent state (*circles*)

first, which was observed on 78 (72.9%) of 107 teliospores with only one germinated cell. The life cycle requires approximately 20 days.

Disease symptoms and teliospore germination

Inoculation experiments showed that teliospores may germinate (and infect other plants) at 10° and 20°C (but not at 6°C), and high humidity. In general, sori of *P. glechomatis* were as large as 1.5 mm in diameter and were scattered over the abaxial surface and occasionally over the adaxial surface of the leaf blade and on the petiole. At high inoculum density, the entire leaf became yellow and then turned brown and necrotic. However, the plants always survived, even with heavy infection. Leaves with only a few sori were asymptomatic other than local discoloration. Very few herbarium specimens revealed what appeared to be a hypersensitive reaction (formation of shot holes) to infection by *P. glechomatis*, but as a rule the telia remained attached to the host. Also, shot hole-like structures were never seen on artificially infected plants.

The fungus may form two different types of teliospores: a pale, thin-walled type germinating at once (leptospore) and a brown, thick-walled type (Fig. 7). The average wall thickness of pale spores was 1.77 µm (SE 0.057, $\alpha = 0.05$) and 2.22 µm (SE 0.069, $\alpha = 0.05$) for brown spores, a difference of 0.55 µm (SE = 0.13, $\alpha = 0.05$).

The study of herbarium specimens from the Midwest of the United States and from Central Europe revealed that sori formed in spring and early summer contained mainly or only leptospores; those collected in fall contained mainly or only thick-walled spores. In the summer months (July, August), both spore types were often formed together in one sorus (Fig. 7) or in different sori on one leaf. In sori formed in late autumn of the previous year and collected in spring, we observed germinating thick-walled teliospores, which indicates that thick-walled spores remain viable after overwintering and function as resting spores. In the greenhouse with temperatures constantly at 18°C ± 2°C, only leptospores were formed.

Spread and distribution

The examination of more than 1400 herbarium specimens of *G. hederacea* revealed 10 records of the fungus. An additional 30 records were collected by collectors who were looking specifically for this rust (mainly from 2000 to 2002).

Figure 12 shows all records of *P. glechomatis* in the United States and indicates the year of the first record in each state. The first record is from May 1992 from Tioga County, Pennsylvania (specimen in CM). In 1993 the fungus was collected for the first time in Indiana and Virginia, in 1994 in West Virginia, in 1996 in Ohio, in 1997 in Kentucky, and in 1998 in New York. In 1998 it appeared also for the first time in Washington State on the West Coast. As of May 2002, the fungus also had been reported in other midwestern states and Oregon. In approximately 10 years, the fungus migrated (or was transported) about 1200 km from Pennsylvania to southern Wisconsin at an average rate of about 120 km per year. In 2002, *P. glechomatis* was found in an area of about 1.5 million km^2 from the East Coast to the Midwest and in a small area on the West Coast of the United States but not in Canada.

Discussion

Böllmann and Scholler (2004) demonstrated that *Glechoma hederacea* was progressing westward in North America at a rate as great as 50 km per year, which the authors explained occurred by human-aided dispersal of vegetative fragments. The total number of 40 records for *P. glechomatis* is comparatively small; they are, however, sufficient data to document distribution and spread of the rust to a certain degree. We assume that *P. glechomatis* was introduced in the north-

eastern United States in the 1980s and has been spread very quickly westward. The average rate of spread of about 120 km per year, however, cannot be explained with fungal diaspores. Neither teliospores (persistent pedicels) nor basidiospores (low weight, thin cell walls, no pigmentation, no cell wall ornamentation, short viability) comply with the requirements of long-distance diaspores dispersed by the wind. The low height of the creeping stems (usually less than 15 cm above the ground) makes a long-distance dispersal even less likely. Basidiospores may serve as short-distance diaspores; the wind most likely transports them no more than a couple of meters, because neighboring "patches" of plants often remained uninfected, and even within one "patch" sometimes only few plants were infected. Given that the fungus produces up to 10 generations per year and assuming the maximum spore dispersal is 100 m, the theoretical maximal annual spread is 1 km, which is an enormous contrast to the calculated 120 km/year.

The long-distance dispersal of *P. glechomatis* as described above can be explained, in part, by host features. Most likely, the agent of long-distance dispersal for the rust is the plant or plant fragments. Transport of both plant and rust may occur by humans, e.g., when transporting infected plants in nursery stocks, in construction waste, etc. Even fragments of plants may form roots, regenerate, and assist survival of the rust fungus in a new area. But how does the fungus remain associated with the host? Microscopic studies have shown that the fungus is not associated with the host as perennial mycelium as in other neomycete rusts on wild herbaceous plants, e.g., *P. malvacearum*, a species on Malvaceae native to Chile (Gäumann 1951). The mode by which *P. glechomatis* migrates with the host is via attachment of viable teliospores, even to dead plant parts. Teliospores have nondeciduous persistent pedicels that do not dissociate when mature and, thus, the teliospores germinate on the host tissue. This persistent pedicel feature is considered a primitive one by Savile (1976, 1978), but is undoubtedly important for fast and long-distance spread of rust neomycetes dispersed together with host diaspores.

The much faster spread compared to that of the host in the 19th century may be the result of the highly developed modern transportation systems, which result in more effective long-distance dispersal. Today, for instance, nursery stocks contaminated with *G. hederacea/P. glechomatis* could be transported by car within North America from one coast to the other within a few days. One hundred years ago, nursery stock usually was not transported over such long distances, and traveling times would have been much longer. The modern transportation systems may also explain why *P. glechomatis* required only about one-tenth the time needed by *G. hederacea* to reach the West Coast. Interestingly, the spreading features of *P. glechomatis* bear a great resemblance to those of *Puccinia lagenophorae* Cooke (=*P. distincta* McAlpine), a species from Australia on species of Senecionae that was found first on the West Coast in 2000 (Scholler and Koike 2001), on the East Coast in 2002 (Hernandez et al. 2003), and in the central United States in Oklahoma in 2004 (Littlefield et al. 2005), but not in regions between. The major host of *P. lagenophorae* is the common groundsel (*Senecio vulgaris*). It is, similar to *G. hederacea*, a common weed, particularly in horticultural crops (Müller-Schärer and Wyss 1994). This observation leads us to assume that *P. lagenophorae*, an opsis-form, is, like *P. glechomatis*, dispersed over long distances mainly by human activities and that numerous generations of repeating aeciospores play a minor role in the long-distance dispersal of the species. Importantly, we assume that neither rust species was introduced twice independently on the east and the west coasts.

We have shown that germination of *P. glechomatis* basidia and basidiospores require high humidity. Therefore, climatic features in North American areas covered by the host (high degree of oceanity, semihumid climate) are favorable for *P. glechomatis* as well. We expect that the fungus will sooner or later cover the closed eastern range of host distribution documented by Böllmann and Scholler (2004).

The strong vegetative growth and the capability to regenerate plants from fragments have been mentioned as favorable features of the host for the establishment and spread of *P. glechomatis*. Considering the strong vegetative growth of the host plant, we assume low genetic diversity and that the plants almost uniformly bear genes for susceptibility to the pathogen. Furthermore, *G. hederacea* has a high ecological amplitude (Ellenberg et al. 1992), tolerating environmental changes, and may appear with high abundance in disturbed manmade habitats (Böllmann and Scholler 2004). This high abundance is especially important for short-distance dispersal of basidiospores.

But what are the requirements for the rust? The fungus apparently has a high ecological amplitude as well. *Puccinia glechomatis* forms two different types of teliospores, one pale- and thin walled, germinating at once (so-called leptospores) for reproduction and short-distance dispersal of basidiospores, and one dark- and thick-walled spore adapted for dormancy and protection against drought and temperature extremes. The existence of both spore types in one sorus or in neighboring sori on one leaf over the summer months enables the fungus to switch quickly from reproduction and dispersal to dormancy and vice versa. The fungus may not be able to become established in arid climates because germination requires high humidity as shown in our inoculation experiments. However, teliospores may be transported with the host over long distances, and thick-walled ones will survive over a longer period of time and can eventually germinate when temperature and humidity are favorable.

In our life-cycle studies, we could not document sexual processes such as the migration of a nucleus from a neighboring cell as described by Ashworth (1931) for *P. malvacearum,* another microcyclic species with a similar life cycle (Eriksson 1911; Allen 1933). The formation of binucleate pedicels and teliospore cells seems to be a result of mitotic nuclear division without cell division of the teliospore mother cell, similar to that described for *Puccinia lantanae* Farl. by Ono (2002). Consequently, recombination rate is low and the rust fungus may remain genetically stable and preserve highly successful combinations of genes. Perti-

nent arguments have been made for self-fertilizing plants (Crow 1986). The stability of genes might be even more favorable for monophagous species (as is *P. glechomatis* in North America), whose host is genetically stable as well.

Conclusion

Uncountable plant parasitic fungi are introduced into countries via highly developed international transportation systems. The vast majority of these species may be short lived or emphemeromycetes (Kreisel and Scholler 1994), i.e., species that disappear a short time after introduction even if potential host plants are abundant. Our studies have shown that for microcyclic rust fungi both host and fungal parasite must fulfill certain conditions to allow the fungus to become established and spread successfully over long distances. For a microcyclic rust neomycete on herbaceous plants, which does not produce long-distance spores, the following features seem favorable. Host plant: synanthropic occurrence and dispersal, high abundance, wide ecological amplitude, asexual reproduction/genetic stability, and regeneration of vegetative plant parts; for the rust fungus: asexual reproduction/genetic stability, homothallism in sexually reproducing species (two different compatible mating types need not be sympatric), fast switch from a resting state to a reproductive state and vice versa, and propagation with the host plant.

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Dedicated to Professor Hanns Kreisel on the occasion of his 75th birthday

References

Allen RF (1933) A cytological study of the teliospores, promycelia and sporidia in *Puccinia malvacearum*. Phytopathology 23:572–586

Ashworth D (1931) *Puccinia malvacearum* in monosporidial culture. Trans Br Mycol Soc 16:177–202

Böllmann J, Scholler M (2004) *Glechoma hederacea* (Lamiaceae) in North America: invasion history and current distribution. Fed Rep 115:178–188

Cousens R, Mortimer M (1995) Dynamics of weed populations. Cambridge University Press, Cambridge

Crow JF (1986) Basic concepts in population, quantitative, and evolutionary genetics. Freeman, New York

Crane PE, Hiratsuka Y, Currah RS (2000a) Clarification of the life-cycle of *Chrysomyxa woroninii* on *Ledum* and *Picea*. Mycol Res 104:581–586.

Crane PE, Hiratsuka Y, Currah RS (2000b) Reproductive biology and evidence for water dispersal of teliospores in *Chrysomyxa weirii*, a microcyclic spruce needle rust. Mycologia 92:754–763

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1992) Zeigerwerte von Pflanzen in Mitteleuropa. Scr Geobot 18:1–166

Eriksson J (1911) Der Malvenrost (*Puccinia malvacearum* Mont.), seine Verbreitung, Natur und Entwicklungsgeschichte. Kgl Svenska Vet Akad Handl 47:1–125

Gardner DE (1981) Nuclear behaviour and clarification of the spore stages of *Uromyces koae*. Can J Bot 59:939–946

Gardner DE (1996) *Puccinia rugispora*: an unusual microcyclic rust endemic to Hawaii. Mycologia 88:671–676

Gäumann E (1951) Pflanzliche Infektionslehre. Birkhäuser, Basel

Gregory PH (1973) The microbiology of the atmosphere, 2nd edn. Leonard Hill, Aylesbury, UK

Hernández JR, Daughtrey M, Jens J (2003) Occurrence of the rust disease caused by *Puccinia lagenophorae* on Cineraria in the Americas. Plant Dis 87:1266

Hiratsuka N, Sato T, Katsuya K, Kakishima M, Hiratsuka Y, Kaneko S, Ono Y, Sato S, Harada Y, Hiratsuka T, Nakayama K (1992) The rust flora of Japan. Tsukuba Shuppankai, Ibaraki

Hutchings MJ, Price EAC (1999) *Glechoma hederacea* L. (*Nepeta glechoma* Benth., *N. hederacea* (L.) Trev). J Ecol 87:347–364.

Koike S, Scholler M (2001) First occurrence of a rust fungus on English daisy (*Bellis perennis*). Plant Dis 85:562

Kreisel H, Scholler M (1994) Chronology of phytoparasitic fungi introduced to Germany and adjacent countries. Bot Acta 107:387–392

Littlefield LJ, Marek SM, Tyrl RJ, Winkelmann KS (2005) Morphological and molecular characterization of *Puccinia lagenophorae*, now present in central North America. Ann Appl Biol 147:35–42

Müller-Schärer H, Wyss GS (1994) Das Gemeine Kreuzkraut (*Senecio vulgaris* L.): Problemunkraut und Möglichkeiten der biologischen Bekämpfung. Z Pfl Krankh Pfl Schutz Sonderh 14:201–209

Narisawa K, Yamaoka Y, Katsuya K (1993) Establishment of axenic culture of *Puccinia coronata* var. *coronata* from basidiospores and their nuclear conditions. Trans Mycol Soc Jpn 34:37–45

Ono Y (2002) Life cycle and nuclear behavior in three rust fungi (Uredinales). Mycoscience 43:37–45

Palm ME, Rossmann AY (2003) Invasion pathways of terrestrial plant-inhabiting fungi. In: Ruiz GM, Carlton JT (eds) Invasive species: vectors and management strategies. Island Press, Washington, DC, pp 31–43

Savile DBO (1976) Evolution of the rust fungi (Uredinales) as reflected by their ecological problems. Evol Biol 9:137–207

Savile DBO (1978) Paleoecology and convergent evolution in rust fungi (Uredinales). BioSystems 10:31–36

Scholler M (1996) Die Erysiphales, Pucciniales und Ustilaginales der Vorpommerschen Boddenlandschaft. Ökologisch-floristische, florengeschichtliche und morphologisch-taxonomische Untersuchungen. Regensb Mycol Schr 6:1–325

Scholler M (1999) Obligate phytoparasitic neomycetes in Germany: diversity, distribution, introduction patterns, and consequences. Texte Umweltbundesamt 18:64–75

Scholler M (2000) Rust on ground-ivy found for the first time in North America. Plant Dis 84:371

Scholler M, Koike S (2001) First occurrence of *Puccinia lagenophorae* causing rust disease on groundsel in North America. Plant Dis 85:335

Sydow P, Sydow H (1904) Monographia Uredinearum, vol 1: genus *Puccinia*. Borntraeger, Leipzig

Uva RH, Neal JC, DiTomaso JM (1997) Weeds of the Northeast. Cornell University Press, New York

Zhuang, J-Y (2003) Flora Fungorum Sinicorum, vol 19. Uredinales (II). Science Press, Beijing