

Ecology, seasonal variation, and altitudinal distribution of Costa Rican smut fungi (Basidiomycetes: Ustilaginales and Tilletiales)*

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Abstract: On the basis of more than 430 collections of Costa Rican smut fungi (Ustilaginales and Tilletiales, Basidiomycetes) and literature, 53 different smut species in 18 genera are listed for the country. *Tilletia ayresii* on *Panicum maximum* is the most frequently collected smut. Apart from some other frequent species, many smut species have rarely been found, though their host plants are frequently met. Most of the smut infections were found on herbaceous hosts (Poaceae and Cyperaceae), in rural vegetation, during the rainy season until the beginning of the dry season. On Cyperaceae, *Anthracoidia* and *Farysia* species occur in the highlands while species of *Cintractia* are mostly restricted to the lowlands. *Cintractia limitata* has only been found below 600 m in Costa Rica, though its host, *Cyperus rotundus*, has been observed frequently at about 1200 m. The distribution of certain smut species and genera shows affinities between the vegetation in tropical highlands and vegetation in temperate climate. Smuts are rarely found on active volcanoes, perhaps because of volcanic air contamination.

Key words: Parasitic fungi, frequency of smut infection, volcano vegetation, aerial pollution, tropics.

Costa Rica, a Central American country of 51900 km² between Nicaragua and Panama, presents many different life zones in coastal plains, hills, valleys, and cordilleras up to 3800 m above sea level. Volcanic activity can be found in the Cordillera de Tilarán and the Cordillera Central. Within the latter, the Poás (2706 m) and the Irazú (3432 m) are active volcanoes, while the volcano Barva (2904 m) is extinct. Most of the Costa Rican people live in the healthy climate of the Central Valley, 1000-1500 m above sea level in the center of the country. On the Pacific side and in the Central Valley, a dry season (January to April) can be distinguished from a rainy season (May to December). About 15 % of the country's surface is mostly primary vegetation in National Parks and other kinds of reserves. The remainder is covered by pastures, sometimes very extensive cultivations, human settlements, and secondary vegetation on bold land. More than 8700 different species of vascular plants have been collected in Costa Rica (Hammel *et al.* 1994), but only about 16 species of smut fungi were mentioned for this country until 1989 (Clinton 1902, Sydow 1925, 1926, Ling 1951, Zundel 1953, Durán and Fischer 1961, Vakili 1978, Gamboa 1989).

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Our knowledge of parasitic fungi in all Mesoamerica is very meager, as has been demonstrated for rust fungi (Uredinales, Basidiomycetes) by Hennen and McCain (1993).

Worldwide, ca. 1300 known species of smut fungi are classified in ca. 50 genera. They mostly infect herbs: 60 % of the host species are Poaceae, 12 % Cyperaceae (Vánky and Oberwinkler 1994). Smuts therefore are most frequently encountered in herbaceous vegetation, but forest plants have also been examined by the author, to make sure that the prevalence of known smuts on herbs is not due to less collecting activity among woody plants.

While smut species of economic importance on cultivated plants are rather well known, information about the numerous smut species attacking wild plants, especially in remote tropical areas, is very scanty. Many species are known only by a short description without further data on their distribution, frequency, and ecological context.

Based on recent collecting activity, new combinations, species, and genera based on 13 different Costa Rican species have been published in Vánky and Bauer (1992), Vánky (1992, 1993, and 1994a), Piepenbring (1995 and 1995a), and Piepenbring *et al.* (1996). Herbarium specimens from Costa Rica were distributed by Vánky

(1992a). Fifty-three Costa Rican smut species are known to attack 57 host species (Piepenbring 1994 and 1996). Some smut species can be found on more than one host species, some species of host plants are hosts for different smut species.

MATERIALS AND METHODS

The results presented here are based on about 400 collections made from 1987 to 1995 by P. Döbbeler (PD), K. Vánky (KV), the author (MP), and some local botanists. Many different parts of Costa Rica have been visited, but areas like the Chirripó mountains, Santa Rosa, the Northern part of the Cordillera de Tilarán, and many less accessible regions remain to be investigated. On the other hand, areas like the Central Valley, the surroundings of Turrialba (Cartago Prov.), and the Interamerican Highway at the Cerro de la Muerte have been repeatedly visited. The collecting activity was focused on smuts on wild plants. Smuts on cultivated plants, which are mentioned for Costa Rica in Gamboa (1989), were collected when seen, but not looked for very often. Twenty-three smut collections were found on their respective hosts in the Herbario del Museo Nacional de Costa Rica (CR) and in the Herbario de la Escuela de Biología, Universidad de Costa Rica (USJ). Other data are taken from literature.

Duplicates of the smut fungi are deposited in the Herbario de Hongos of the Escuela de Biología of the Universidad de Costa Rica (USJ), in the Herbarium Botanische Staatssammlung München (M), in the Herb. Ustilag. Vánky (H.U.V.), and in the Herb. Ustilag. Piepenbring (H.U.P.; MP numbers are collection numbers of the author, H.U.P. numbers are inventory numbers of the herbarium). One healthy specimen of each host plant species of Costa Rican smuts is deposited in CR. The altitudinal distribution of certain host plants is cited from the respective descriptions in the Flora Mesoamericana (Davidse *et al.* 1994).

The following list contains only the data of collections which are cited in the text. Complete collection data are published in Piepenbring (1994, 1996). Taxonomic authorities are mentioned in the list (see results).

Anthracoidea altiphila on *Carex chordalis*: Prov. Cartago, Cerro de la Muerte, Tres de Junio, 2600 m, 11-X-1992, L. Umaña & M. Piepenbring 397. On *Carex jamesonii*: Prov. San José, Chirripó National Park, Crestones Valley, 3350 m, 26-III-1983, A. Chaverri, A. Cleef, & R. Madrigal (CR 96857: on *C. cortesii*).

Anthracoidea pannucea on *Carex bonplandii*: Prov. Alajuela, Poás, 2700 m, 13-IV-1976, R. Chazdon (CR 61955). Prov. Cartago, Cerro Asunción, 3200 m, 28-I-1981, J. Gómez-Laurito (CR 80349); 15 km S Cartago, Empalme, La Chonta, 2000 m, F. Oberwinkler & R. Berndt (H.U.V. 14095). Prov. Heredia, Volcán Barva, park administration, 2610 m, 16-XII-1993, G. Rivera & M. Piepenbring 993; Volcán Barva, summit, 2660 m, 17-XII-1993, G. Rivera & M. Piepenbring 994.

Cintractia axicola on *Fimbristylis dichotoma*: Prov. Puntarenas, Ballena, Uvita, 2 m, 3-VII-1993, G. Rivera & M. Piepenbring 933. Prov. San José, San Francisco de Dos Ríos, El Bosque, 1150 m, 26-XII-1993, G. Rivera & M. Piepenbring 1000.

Cintractia fimbristylicola on *Fimbristylis spadicea*: Prov. Guanacaste, 8 km SW La Cruz, Puerto Soley, 1 m, 19-X-1992, M. Piepenbring 471.

Cintractia leucoderma on *Rhynchospora holoschoenoides*: Prov. Alajuela, Caño Negro, 80 m, 26-III-1991, T. & K. Vánky (H.U.P. 266).

Cintractia limitata on *Cyperus rotundus*: Prov. Puntarenas, Puntarenas, 2 m, 14-X-1992, M. Piepenbring 418 and 419. On *Torulinium odoratum*: Prov. Cartago, Atirro, S Turrialba, 550 m (not "ca. 1300 m" indicated in the herbarium), 3-VI-1966, A. S. Weston (CR 87560).

Cintractia scleriae on *Rhynchospora corymbosa*: Prov. Alajuela, 14 km SE Los Chiles, 90 m, 24-III-1991, T. & K. Vánky (H.U.P. 274). Prov. Limón, Barra del Colorado, 1 m, 26-VI-1993, M. Piepenbring 893.

Entorrhiza aschersoniana on *Juncus bufonius*: Prov. Cartago, volcanso Irazú, 50 km E San José, 2970 m, L. Horovitz, T. & K. Vánky (H.U.P. 310).

Entorrhiza casparyana on *Juncus tenuis*: Prov. Cartago, 45 km S San José, 1930 m, 30-XI-1992, C. Rivera & M. Piepenbring 742.

Entyloma australe on *Physalis cordata*: Prov. San José, between Las Nubes and Cascajal de Coronado, 1700-1900 m, 14-VI-1980, J. Gómez-Laurito (CR 78047).

Entyloma bidentis on *Bidens pilosa*: Prov. San José, Guadalupe, 1200 m, 7-VIII-1991, P. Döbbeler 6497; 9-X-1992, M. Piepenbring 335, 336, and 348; 21-X-1992, M. Piepenbring 488; 26-V-1993, M. Piepenbring 826.

Entyloma microsporium on *Ranunculus pilosus*: Prov. Cartago, near volcano Turrialba, La Pastora, 1600 m, 13-XI-1992, G. Rivera & M. Piepenbring 645.

Farysia chardoniana on *Carex polystachya*: Prov. Heredia, volcano Barva, Paso Llano, Guardia de Asistencia Rural, 1900 m, 16-XII-1993, G. Rivera & M. Piepenbring 992. Prov. San José, Tablazo de Acosta, 1050 m, 29-XI-1992, M. Piepenbring 730.

Farysia corniculata on *Carex jamesonii*: Prov. Cartago, Cerro de la Muerte, Tres de Junio, 2600 m, 1-VII-1993, G. Rivera & M. Piepenbring 913. On *Carex lemmaniana*: Prov. Cartago, Cerro de la Muerte, Cerro Buenavista, 3280-3400 m, 30-VIII-1991, P. Döbbeler 6529.

Mycosyrinx cissi on *Cissus sicyoides*: Prov. Cartago, La Suiza, Beré Beré de Alto Pacuare, Río Pacuare, 750 m, 5-IX-1994, G. Rivera & M. Piepenbring 1180. On *Cissus* sp.: Prov. Limón, Alto Coën, Talamanca, Río Coën, III-1978, R. A. Ocampo S. & C. Todzia (CR 106492).

Rhamphospora nymphaeae on *Nymphaea ampla*: Prov. Guanacaste, National Park Palo Verde, OTS station, 5 m, 17-XI-1992, A. Schumacher & M. Piepenbring 675; 16 km SW Cañas, Taboga, 50 m, 15-VI-1993, M. Piepenbring 890.

Thecaphora haumani on *Iresine diffusa*: Prov. Cartago, La Suiza, Beré Beré de Alto Pacuare, 800 m, 5-IX-1994, G. Rivera & M. Piepenbring 1178.

Tilletia ayresii [in H.U.V. and Vánky, Ust. Exs. as *Conidiosporomyces ayresii* (Berkeley) Vánky] on *Panicum maximum*: Prov. Cartago, between Cachí and Tukurrique, 0.5 km S San Jerónimo, 1000 m, 28-IX-1991, P. Döbbeler 6502; 5 km W Sabanilla near Tukurrique, 950 m, 28-IX-1991, P. Döbbeler 6503; between Paraíso and Ujarrás, 1240 m, 28-IX-1991, P. Döbbeler 6505; Valle de Orosi, 1100 m, 12-X-1992, R. Bandoni & M. Piepenbring 401; 12-VI-1993, G. Kost & M. Piepenbring 863. Prov. Puntarenas, Sierpe, 2 m, 1-VII-1993, G. Rivera & M. Piepenbring 928. Prov. San José, Coronado, 1380 m, 1-XI-1992, M. Piepenbring 553.

Urocystis ranunculi on *Ranunculus pilosus*: Prov. Cartago, volcán Turrialba, between Pacayas and Santa Cruz, 2350 m, 21-IV-1990, P. Döbbeler (USJ 28313; Vánky, Ust. Exs. No. 867).

Ustilago affinis on *Stenotaphrum secundatum*: Prov. San José, San José, avenida central y 1, calle 2, 1150 m, M. Piepenbring 1177.

Ustilago schroeteriana on *Paspalum paniculatum*: Prov. Limón, Bribri, Yorkín, 18-VI-1993, G. Rivera & M. Piepenbring 940; school of Yorkín, 200 m, 21-XII-1993, G. Rivera & M. Piepenbring 996.

Ustilago striiformis on *Holcus lanatus*: Prov. Heredia, 30 km NNW San José, Vara Blanca, 1990 m, 9-III-1991, T. & K. Vánky (H.U.P. 366).

RESULTS AND DISCUSSION

Checklist of Costa Rican smut fungi each with number of collections (coll.) and surrounding vegetation:

Anthracoidea altiphila Vánky and Piepenbring, in Vánky on *Carex chordalis* Liebm. *C. jamesonii* Boott, and *C. lemniiana* Boott - 9 coll. paramo.

A. pannucea (Liro) Vánky on *Carex bonplandii* Kunth - 14 coll. highland swamp.

Aurantiosporium subnitens (Schröter and Hennings, in Hennings) Piepenbring, Vánky, and Oberwinkler on *Scleria melaleuca* Reichb. - 12 coll. rural.

Conractia axicola (Berkeley) Cornu on *Fimbristylis dichotoma* (L.) Vahl - 19 coll. moist rural.

C. fimbristylicola Pavgi and Mundkur on *Fimbristylis spadicea* (L.) Vahl - 1 coll. close to the sea.

C. leucoderma (Berkeley) Hennings on *Rhynchospora holoschoenoides* (L. C. Rich.) Herter - 1 coll. moist rural.

C. limitata Clinton on *Cyperus rotundus* L. and *Torulinium odoratum* (L.) S. Hooper - 18 coll. moist rural.

C. scleriae (De Candolle) Ling on *Rhynchospora corymbosa* (L.) Britton - 10 coll. rural swamp.

Doassansiopsis limnocharidis (Ciferri) Vánky on *Limnocharis flava* (L.) Buchenau - 2 coll. rural swamp.

D. ticonis Piepenbring on *Nymphaea blanda* G. F. W. Meyer - 1 coll. swamp.

Entorrhiza aschersoniana (P. Magnus) Lagerheim on *Juncus bufonius* L. - 1 coll. moist rural.

E. casparyana (P. Magnus) Lagerheim on *Juncus tenuis* Willd. - 1 coll. moist rural.

Entyloma australe Spegazzini on *Physalis cordata* Miller - 1 coll. rural.

E. bidentis Hennings, in Engler on *Bidens pilosa* L. - 36 coll. rural.

E. browalliae H. Sydow on *Browallia americana* L. - 10 coll. moist rural.

E. compositarum Farlow on *Viguiera cordata* (Hook. and Arn.) d'Arcy and *V. sylvatica* Klatt - 3 coll. moist rural.

E. dahliae H. and P. Sydow on *Dahlia* sp. cult. - 16 coll. rural.

E. delileae Vánky, Döbbeler, and U. Braun, in Vánky on *Delileia biflora* (D. C.) Spreng. - 3 coll. rural.

E. doebbeleri Piepenbring on *Dahlia* sp. cult. and *Dahlia imperialis* Roetzi - 14 coll. rural.

E. ecuadorensis H. Sydow on *Acmella oppositifolia* (Lam.) R. K. Jansen var. *oppositifolia* - 14 coll. rural.

E. galinsogae H. and P. Sydow on *Galinsoga urticaefolia* (H.B.K.) Benth. - 4 coll. moist rural.

E. lobeliae Farlow on *Lobelia laxiflora* H.B.K. - 1 coll. rural.

E. microsporum (Unger) Schröter, in Rabenhorst on *Ranunculus pilosus* H.B.K. - 17 coll. moist rural.

E. oryzae H. and P. Sydow on *Oryza sativa* L. (cult.) - reported in literature, cultivated.

E. vignae Batista, Bezerra, Ponte, and Vasconcelos on *Phaseolus vulgaris* L. (cult.) - reported in literature, cultivated.

Farysia chardoniana Zundel on *Carex polystachya* Swartz ex Wahlenb. - 19 coll. secondary forest.

F. corniculata Vánky on *Carex chordalis* Liebm. *C. jamesonii* Boott, and *C. lemniiana* Boott - 9 coll. paramo.

Melanopsichium pennsylvanicum Hirschhorn on *Polygonum hispidum* H.B.K. - 1 coll. moist rural.

Mycosyrinx cissi (De Candolle) G. Beck on *Cissus rhombifolia* Vahl and *C. sicyoides* L. - 16 coll. secondary vegetation and primary forest.

Rhamphospora nymphaeae D. Cunningham on *Nymphaea ampla* (Salisb.) D.C. - 2 coll. rural ponds.

Sphacelotheca cf. *hydropiperis* (Schumacher) De Bary on *Polygonum acuminatum* H.B.K. and *P. punctatum* Elliot - 35 coll. moist rural.

Sporisorium cruentum (Kühn) Vánky on *Sorghum bicolor* (L.) Moench (cult.) - reported in literature, cultivated.

S. culmiperdum (Schröter) Vánky on *Andropogon bicornis* L. and *A. glomeratus* (Walt.) B. S. P. - 7 coll. rural.

S. holwayi (Clinton and Zundel) Vánky on *Andropogon bicornis* L. - 3 coll. rural.

S. reilianum (Kühn) Langdon and Fullerton on *Sorghum bicolor* (L.) Moench (cult.) - reported in literature, cultivated.

S. sorghi Ehrenberg ex Link on *Sorghum bicolor* (L.) Moench (cult.) - reported in literature, cultivated.

S. veracruzianum (Zundel and Dunlap) Piepenbring on *Panicum viscidellum* Scribn. - 2 coll. rural.

Thecaphora haumani Spegazzini on *Iresine diffusa* Humb. and Bonpl. ex Willd. - 2 coll. rural.

T. pustulata Clinton, in Chardón on *Bidens pilosa* L. - reported in literature, rural.

Tilletia ayresii Berkeley, in Massee on *Panicum maximum* Jacq. and *Setaria paniculifera* (Steud.) Fourn. - 70 coll. rural.

T. oplismeni-cristati Patouillard and Harris, in Durán and Fischer on *Oplismenus burmannii* (Retz.) Beauv. - reported in literature, rural.

Tolyposporium rhynchosporae-cephalotis K. and T. Vánky, in K. Vánky on *Rhynchospora cephalotes* (L.) Vahl - 2 coll. rural.

Trichocintractia utriculicola (Hennings) Piepenbring on *Rhynchospora corymbosa* (L.) Britton - 13 coll. rural swamp.

Urocystis ranunculi (Libert) Moesz on *Ranunculus pilosus* H.B.K. - 1 coll. moist rural.

Ustilago affinis Ellis and Everhart, in Cockerell on *Stenotaphrum secundatum* (Walt.) Kuntze - 4 coll. rural.

U. ixophori Durán on *Ixophorus unisetus* (Presl.) Schlecht. - 1 coll. rural.

U. maydis (De Candolle) Corda on *Zea mays* L. (cult.) - 3 coll. cultivated.

U. montagnei L.R. and C. Tulasne on *Rhynchospora globosa* (Kunth) Roemer and Schultes - 3 coll. savanna.

U. schroeteriana Hennings on *Paspalum conjugatum* Bergius, *P. costaricense* Mez, *P.*

paniculatum L. *P. plicatum* Michx. and *P. virgatum* L. - 25 coll. rural.

U. scitaminea H. Sydow on *Saccharum officinarum* L. (cult.) - 3 coll. cultivated.

U. striiformis (Westendorp) Niessl on *Holcus lanatus* L. - 1 coll. rural.

U. tenuispora Ciferri on *Polygonum punctatum* Elliot - 2 coll. moist rural.

U. tillandsiae Patterson, in Clinton on *Tillandsia costaricana* Mes. and Werckle - reported in literature.

Frequency of smut occurrence: *Tilletia ayresii* on *Panicum maximum* and sometimes on *Setaria paniculifera* is the most frequently collected smut in Costa Rica (70 coll.). The extraordinary success of *T. ayresii* might be explained by the commonness of the host *P. maximum*, an African forage grass, and by balls of conidia which are vegetative diaspores formed by this smut in addition to the teliospores. In contrast to the thick-walled teliospores, the conidia germinate very quickly (Vánky and Bauer 1992).

Other frequent hosts and smuts are *Bidens pilosa* with *Entyloma bidentis* (36 coll.), *Polygonum punctatum* with *Sphacelotheca* cf. *hydropiperis* (35 coll.), and *Paspalum* spp. with *Ustilago schroeteriana* (25 coll.). However, many smut species are difficult to find albeit their hosts are common: *Entyloma delileae*, *E. galinsogae*, *Sporisorium culmiperdum*, *S. holwayi*, *S. veracruzianum*, *Thecaphora haumani*, *Urocystis ranunculi*, *Ustilago striiformis*, and *U. tenuispora*. In the case of *Cintractia fimbristylicola*, only a single group of host plants in a restricted area of an estuary with a huge population of *Fimbristylis spadicea* was found to be infected (MP 471). Ten smut species have been found only once since 1987.

The very sporadic incidence of certain smut species might be attributed to the rather unlikely coincidence of viable teliospores or other dispersal units getting onto a penetrable organ of a host plant of low resistance in an environment favorable for teliospore germination and the production of infective cells. The fact that most of the recorded host plants are very frequent in Costa Rica and the possible development of smut plagues in monocultures without control measures show that a high density of host plant individuals is important for the survival of the respective smut species. Complex experiments are necessary to estimate the importance of humidity,

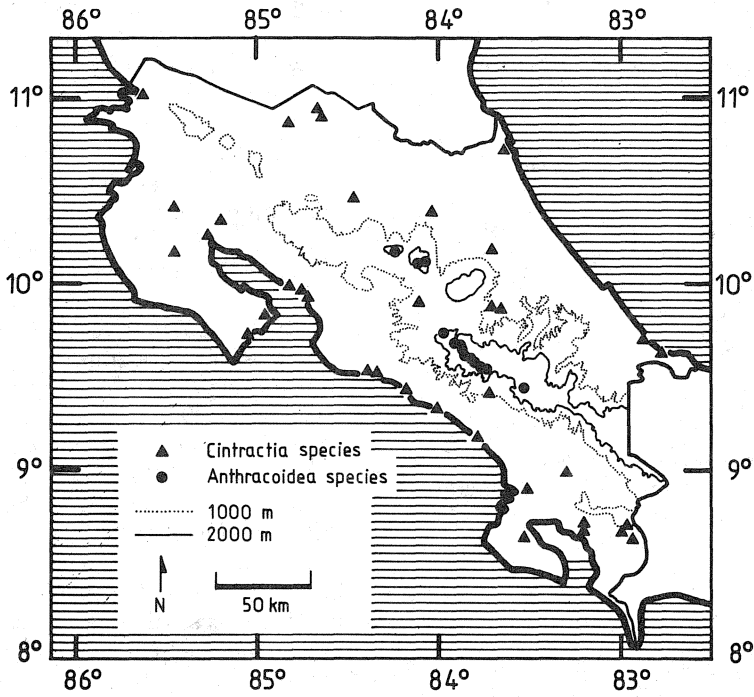


Fig. 1. Location of collections of *Cintractia* spp. and *Anthracoidea* spp. in Costa Rica in relation to altitudinal levels.

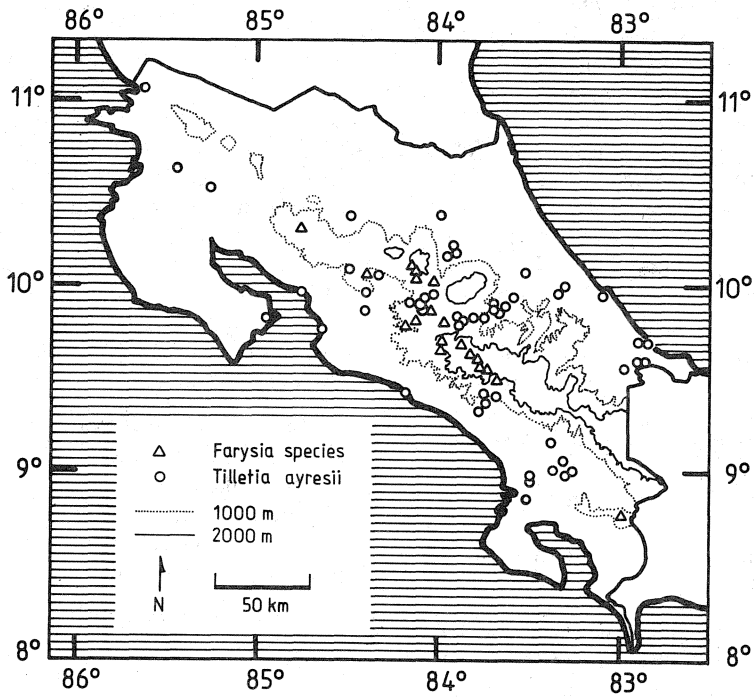


Fig. 2. Location of collections of *Farysia* spp. and *Tilletia ayresii* in Costa Rica in relation to altitudinal levels.

temperature, wind, irradiation, the physiological constitution of the interacting organisms, and other factors affecting the success of smut infection.

Certain smut species have seldom been collected because they are easily overlooked, e. g. *Entorrhiza* spp. in tiny galls of roots of Juncaceae and Cyperaceae and *Entyloma* spp. causing leaf spots which are difficult to see or difficult to distinguish from spots due to other agents. *Thecaphora pustulata* and *Tilletia oplismeniscristati* known for Costa Rica by literature (Ling 1951, Durán and Fischer 1961) as well as *Entyloma australe* from a herbarium specimen (CR 78047) could not be found, though their hosts have been examined repeatedly. Few *Tillandsia* plants were examined for the (doubtful) smut *Ustilago tillandsiae* reported from Costa Rica by Clinton (1902), but the fungus was not found.

Surrounding vegetation: Thirty-nine of the 53 Costa Rican smuts (ca. 74 %) can be found in rural, secondary, mostly herbaceous vegetation. They grow along roads, paths, fields, pastures, in villages, and even in the middle of cities like San José (*Ustilago affinis*, MP 1177). The sites often are moist, sometimes swampy. Six species are known to attack cultivated plants in Costa Rica. *Anthracoidea altiphila* and *Farysia corniculata* are typical for the paramo, where their hosts mostly grow in open areas like those at the Panamerican Highway. The only known smut host plants, that occur naturally in the Costa Rican rain forests and have been found infected there, are *Cissus* spp. vines with *Mycosyrinx cissi* (CR 106492, MP 1180). However, within the forest *Cissus* grows mainly in areas with some sunlight, like gaps or riversides. Many other Costa Rican *M. cissi* collections stem from *Cissus* in rural vegetation at roadsides. *Thecaphora haumani* and *Ustilago schroeteriana* have been found on their respective host plants surrounded by rain forest in indigenous settlements of Beré Beré de Alto Pacuare (MP 1178) and Yorkín at the Panamanian border (MP 940 and 996) respectively.

The prevalence of smuts in rural vegetation may be explained by the presence of many individuals of a few herbaceous species, some of them smut hosts, and by open spaces accessible to teliospores dispersed by wind. The high number of

smut collections from rural areas also results from the fact that those sites are the most easily accessible places to look for smuts. No smut could be found on trees.

Seasonal variation: The best time for smut collecting seems to be from the middle of the rainy season until the beginning of the dry season. By the end of the dry season it can be very difficult to find smuts. Seasonal variation has been observed for *Tilletia ayresii* on several visits to the Orosí Reventazón valley close to Paraíso (Cartago province). In September and October of 1991 and 1992, towards the end of the rainy season, *Panicum maximum* at the roadside was heavily infected (PD 6502, 6503, 6505; MP 401), while in June of 1993, at the beginning of the rainy season, many *P. maximum* plants were sterile, others had apparently healthy young inflorescences, and infection could be found in old inflorescences only in a restricted area (MP 863). Teliospores and conidia of the few infected host plants or infective cells from germinated teliospores on the ground probably can infect the young inflorescences. The smut seems to need a certain period of time at the beginning of the rainy season to get established in the large population of host plants.

A similar seasonal variation has been observed in the case of *Entyloma bidentis* on *Bidens pilosa* in Guadalupe close to San José. In the rainy season the leaf spots were often noticed (PD 6497, MP 335, 336, 348, 488, 826), while in the dry season the host plants are mostly healthy, although they present green leaves which seem to be susceptible to smut infection. The importance of humidity for successful infection is well known for *Entyloma* species, for example in the case of *E. ranunculi* Bonorden (= *E. ficariae* Thümen ex Fischer v. Waldheim) as noticed by Ward (1887).

Smut occurrence from the middle of the rainy season to the beginning of the dry season seems to be due to the presence of extensive flowering host populations at this time and high humidity favorable for teliospore germination, fungal growth, and infection.

On the Caribbean side of Costa Rica where there is no harsh dry season, the surroundings of Turrialba (CATIE, Atirro, Guayabo) have been visited repeatedly. They have the highest species count (14): *Cintractia axicola*, *C. limitata*, *Entyloma bidentis*, *E. compositarum*, *E. dahliae*,

E. galinsogae, *E. microsporum*, *Mycosyrinx cissi*, *Sphacelotheca* cf. *hydropiperis*, *Thecaphora haumani*, *T. pustulata*, *Tilletia ayresii*, *Urocystis ranunculi*, and *Ustilago schroeteriana*. The high number of species is probably related to the very humid climate of the region. Seasonal variation remains to be investigated.

Altitudinal distribution: Among the Costa Rican smut species, *Entorrhiza aschersoniana* (H.U.P. 310), *E. casparyana* (MP 742), *Entyloma microsporum* (MP 645), *Urocystis ranunculi* (USJ 28313), and *Ustilago striiformis* (H.U.P. 366) occur at high elevations: the cited collections at 1600-3000 m. These smut species also are known in temperate zones, where the summer climate corresponds roughly to the climate at higher elevations in the tropics. The host of *U. striiformis*, *Holcus lanatus*, and the host of *E. aschersoniana*, *Juncus bufonius*, are native in more or less temperate zones (Bernhardt and Koch 1994). They probably have been introduced to the tropical highlands together with their smuts. The worldwide known *Rhizophora nymphaeae*, has been collected twice on *Nymphaea ampla* in Costa Rican lowland swamps (MP 675, 890; at 5 and 50 m respectively). At higher altitudes, *N. ampla* was sometimes observed only healthy. Obviously, the rule that smut species known from temperate zones occur in tropical highlands has to permit exceptions.

Among the repeatedly collected Costa Rican smut taxa, species of *Anthracoidea*, *Cintractia*, and *Farysia* on Cyperaceae show distinct altitudinal distributions. Figs. 1 and 2 show the locations of collections of these smuts, as well as the collection sites of the most frequent species, *Tilletia ayresii*, in relation to different altitudinal levels. All the specimens of *Anthracoidea* species have been collected at at least 2000 m above sea level (Fig. 1). Collections of *A. pannucea* are from 2000-3200 m (altitudes from H.U.V. 14095 and CR 80349), those of *A. altiphila* from 2600-3400 m (MP 397 and CR 96857). *Cintractia* species have been collected from sea level to up to 1200 m (Fig. 1). *C. fimbristylicola* was collected once close to the coast (MP 471), *C. leucoderma* once at 80 m (H.U.P. 266), *C. scleriae* from 0-100 m (MP 893 and H.U.P. 274), *C. limitata* from 0-550 m (MP 418 and CR 87560), and *C. axicola* from 0-1200 m (MP 933 and MP 1000). *C. axicola* is the only *Cintractia* species which

has been encountered at more than 600 m. *Farysia* species have been collected in places at least 1000 m above sea level (Fig. 2). *F. corniculata* has been found at 2600-3400 m (MP 913 and PD 6529), *F. chardoniana* at 1000-1900 m (MP 730 and MP 992). The host of *F. chardoniana*, *Carex polystachya*, reaches only to 2400 m, while the *Carex* host species of *F. corniculata* are typical for the paramo region. The genera *Anthracoidea* and *Farysia* include species in temperate zones as well as in tropical latitudes, where they grow mainly at high elevations (for *Anthracoidea* comp. Vánky 1994). Obviously, the distribution rule presented above for some cosmopolite smut species also applies to genera represented by different species in different latitudes. Species of the genus *Cintractia* with a diversification center in the tropics occur mainly in tropical lowland. *Tilletia ayresii* infects *Panicum maximum* from 0-1400 m above sea level (MP 928 and MP 553) in many different parts of the country (Fig. 2). *P. maximum* can grow at up to 2000 m, but was not often seen at this altitude.

While most of the smut infections seem to occur more or less in the whole altitudinal range of the respective host, *Cintractia limitata* on *Cyperus rotundus* and *Torulium odoratum* seems to be restricted to lowland host populations. *C. rotundus* grows from 0-1400 m and has been examined many times at more than 1000 m, especially in the Central Valley where it is a common roadside weed. It has been found only healthy there. Close to sea level (0-120 m) *C. rotundus* can be heavily infected, as it has been observed in Puntarenas in October 1992 (MP 418 and 419). The highest altitude, at which *C. limitata* has been collected, is 550 m at Atirro, Turrialba, on *T. odoratum* in 1966 (CR 87560). The author tried to collect it again in 1995, but only found large populations of healthy *T. odoratum* and some healthy *C. rotundus* in the area. In contrast to *C. limitata*, *C. axicola* was found on its host *Fimbristylis dichotoma* close to sea level, as well as in the San José area (1150 m, MP 1000).

C. limitata has not been found in its maximum geographic range corresponding to the range of its hosts in Costa Rica, probably because it has ecological demands different from those of the host plant. Nannfeldt (1979) describes restrictions in the distribution of certain *Anthracoidea* species in large geographic areas and proposes climatological and historical reasons. In the case of *C. limitata*

climate conditions, which differ decisively at different altitudinal levels, most probably are the reason for the restricted smut incidence. However, further records of infected and healthy host populations, as well as experiments, are necessary to elucidate the factors causing this restricted distribution.

Smuts on volcanoes: In the summit regions of the volcanoes Irazú, Poás, and Barva, the smut host plants *Carex bonplandii*, *C. jamesonii*, *C. lemmaniana*, and *C. polystachya* have been examined. However, smut infection could be found only on top of the extinct volcano Barva (*Anthracoidea pannucea* on *C. bonplandii*; MP 993 and 994). *A. pannucea* has been collected once on the volcano Poás (CR 61955), but neither K. Vánky nor P. Döbbeler nor the author could find any smut on the active volcanoes Irazú and Poás, in spite of repeated searching.

This reduced smut incidence on the summit of active volcanoes might be due to volcanic contamination of the air, especially to high SO₂ concentration. On the volcano Poás, especially in wet cloudy weather the air is charged with volcanic vapor and affects the local vegetation (Macey 1975). The volcanic vapor might inhibit teliospore germination or damage infective smut cells. Aerial pollution also has been suggested as the reason for a decrease of Erysiphales observed in Vorpommern (Germany) by Scholler and Schubert (1993). In the case of Erysiphales and smuts, an experimental verification of the hypothesis is still lacking. For *Rhynisma acerinum*, the agent of tarspot disease, it has been experimentally shown that higher SO₂ concentration inhibits ascospore germination (Bevan and Greenhalgh 1976, Greenhalgh and Bevan 1978, both in Webster 1988).

Costa Rica, a country characterized by numerous vegetation types at 0-3800 m, seems to harbor a correspondingly high variety of smut species. The list of Costa Rican smuts is far from complete, however. Smut species known from other Mesoamerican countries, e. g. *Sporisorium cenchri* (Lagerheim) Vánky on *Cenchrus* spp. and several *Sporisorium* species on *Andropogon* spp. and other grasses, and many other species probably have been overlooked and remain to be discovered. *Ustilago tillandsiae* on *Tillandsia*

spp. should be recollected to verify whether it really is a smut fungus.

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RESUMEN

Con base en más de 430 muestras botánicas de carbones (Ustilaginales y Tilletiales, Basidiomicetes) recolectadas en Costa Rica y en revisión bibliográfica, se registran para este país 53 especies de carbones en 18 géneros. *Tilletia ayresii* en *Panicum maximum* es el carbón que ha sido recolectado en Costa Rica con mayor frecuencia. Hay muchas otras plantas hospederas que se encuentran en abundancia pero sus parásitos las infectan rara vez. La mayor parte de las plantas hospederas son hierbas rurales (gramíneas y ciperáceas). El período más adecuado para encontrar carbones parece ser el período comprendido entre la época húmeda y el comienzo de la época seca. En plantas hospederas de ciperáceas, las especies costarricenses de los géneros *Anthracoidea* y *Farysia* se presentan en tierras altas mientras que *Cintractia* spp. están sobre todo en tierras bajas. *Cintractia limitata* ha sido encontrada en Costa Rica hasta ahora únicamente en altitudes menores de 600 m aunque su hospedero, *Cyperus rotundus*, ha sido examinado muchas veces en altitudes de 1200 ± 100 m. Ciertas especies y géneros de carbones que se conocen en la zona templada se encuentran exclusivamente en las regiones altas de la zona tropical. Casi no hay carbones cerca de las cimas de volcanes activos, tal vez debido a la contaminación volcánica del aire.

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