

Cannabis* pathogens XI: *Septoria* spp. on *Cannabis sativa*, *sensu stricto

John M. McPartland

Vermont Alternative Medicine/AMRITA, Middlebury, VT 05753, U.S.A.

McPartland, J. M. (1995). *Cannabis* pathogens XI: *Septoria* spp. on *Cannabis sativa*, *sensu stricto*. – *Sydowia* 47 (1): 44–53.

Two species of *Septoria* on *C. sativa* are described and contrasted. *S. cannabina* Westendorp and *Spilosphaeria cannabis* Rabenhorst become synonyms of *S. cannabis* (Lasch) Saccardo. *S. cannabina* Peck is illegitimate, *S. neocannabina* nom. nov. takes its place; *Septoria cannabis* var. *microspora* Briosi & Cavara becomes a synonym therein. *S. graminum* Desmazières is not considered a *Cannabis* pathogen; '*Cylindrosporium* sp.' on hemp is a specimen of *S. neocannabina*, *Rhabdospora cannabina* Fautrey is discussed.

Keywords: *Cannabis sativa*, *Cylindrosporium*, exsiccata, *Septoria*, taxonomy.

The genus *Septoria* Saccardo is quite unwieldy, containing about 2000 taxa. Sutton (1980) notes some workers have subdivided and studied the genus by geographical area. Grouping *Septoria* spp. by their host range is a more natural way of studying the genus in surmountable subunits. Six previous papers have revised *Septoria* spp. based on host studies (Punithalingham & Wheeler, 1965; Constantinescu, 1984; Sutton & Pascoe, 1987; Farr, 1991, 1992a, 1992b). Their results suggest *Septoria* host ranges are limited, and support the continued study of *Septoria* by host groupings. These compilations and comparisons are especially useful when cultures are lacking.

Several species of *Septoria* reportedly cause yellow leaf spot on *Cannabis* (McPartland, 1991). Together they make this disease nearly ubiquitous; it occurs on every continent save Antarctica. The U.S. National Fungus Collections (BPI) contain 61 collections of *Septoria* spp. on *Cannabis* in its general collection (not counting exsiccata sets); these collections twice outnumber those of any other *Cannabis* pathogen.

The genus *Cannabis* may be monotypic (*C. sativa* L., *apud* Small & Cronquist, 1976) or polytypic (*C. sativa* for fiber varieties, *C. indica* Lamarck for euphoriant, and *C. ruderalis* Janischevsky for primeval non-cultivated plants, *apud* Schultes & al., 1974). Persoon was the first to synonymize *C. indica* under *C. sativa* (McPartland, 1992).

Circumventing this debate, I only examined collections from fiber varieties (*C. sativa sensu stricto*). For the record, yellow leaf spot has been cited on euphoriant varieties (Ghani & al., 1978; Mushtaque & al., 1973) and *C. ruderalis* (Szembel, 1927; Gamalitskaia, 1964).

S. graminum Desmazières cited on *C. sativa* can safely be ignored as an error. Rataj (1957) describes this pathogen on Czechoslovakian hemp. *S. graminum* has only been reported from monocots; infesting a dicot host like *Cannabis* is improbable. Eliminating this suspect citation leaves six other taxa: *S. cannabis* (Lasch) Saccardo, *S. cannabina* Westendorp, *Spilosphaeria cannabis* Rabenhorst, *S. cannabina* Peck, *S. cannabis* var. *microspora* Briosi & Cavara, and *Rhabdospora cannabina* Fautrey.

Materials and methods

Conidiomata were dislodged from leaf fragments with dissecting needles and rehydrated in 3% KOH, then measured at their widest part. They were either hand-sectioned with a razor blade or teased apart with needles under a 4x objective. Material was stained with either cotton blue in lactic acid or 1% phloxine in water (phloxine subsequently replaced with KOH by capillary action under a cover slip). Curved conidia were measured along their circumference, widths measured at their widest part, and means determined from 50 conidia.

Specimens for SEM were fixed in 4% gluteraldehyde (in 0.1 M cacodylate buffer), dehydrated in a graded ethanol series, critical-point dried with CO₂, sputter coated with gold palladium, and examined with an Amray 1200B SEM operating at 30kV.

Collections examined.—

S. cannabis (Lasch) Saccardo. — LECTOTYPE: GERMANY, Driesen, as '*Ascochyta cannabis* Lasch' in Rabenhorst's Klotzchii Herbarium vivum mycologicum, Editio Nova, exsiccatum no. 1509, 1846 (B). GERMANY: Driesen, as '*Ascochyta cannabis* Lasch' in Rabenhorst's Klotzchii Herbarium vivum mycologicum, Editio Nova, exsiccatus no. 1509, 1846 (BPI). — NEPAL: Ghorapani, J.M. McPartland, October 1986 (BPI); Kathmandu, J.M. McPartland, October 1986 (BPI); Jomson, J.M. McPartland, October 1986 (BPI).

S. cannabina Westendorp. — HOLOTYPE: BELGIUM, Beverloo, G.D. Westendorp, 1857 (BR). — UNITED STATES: Kewanee, IL, G.H. Boewe, 14.9.1937 (ILLS); New Windsor, IL, G.H. Boewe, 28.10.1936 (ILLS).

Sp. cannabis Rabenhorst. — HOLOTYPE: GERMANY, Giessen, Rabenhorst Herbarium vivum mycologicum, Editio II, exsiccatum no. 559, leg. Hofmann, 1857 (B). — GERMANY: Giessen, Rabenhorst Herbarium vivum mycologicum, Edition II, exsiccatum no. 559, leg. Hofmann, 1857 (BPI).

S. cannabina Peck. — HOLOTYPE: UNITED STATES, Cold Spring, NY, C.H. Peck, 5.1884 (NYS). UNITED STATES: Yarrow, MD, labeled '*Cylindrosporium* sp.', J.T. Rogers, 17.6.1917 (BPI).

S. cannabis var. *microspora* Briosi & Cavara. – LECTOTYPE: ITALY, Pavia, I Funghi Parassiti Delle Piante Coltivate Od Utili, exsiccatum no. 94, 1888 (PAV). – SYNTYPE: ITALY, Pavia, I Funghi Parassiti Delle Piante Coltivate Od Utili, exsiccatum no. 94, 1888 (BPI).

R. cannabina Fautrey. – AUSTRIA: Tirol, Völs bei Innsbruck, Reliquiae Petrakianae no. 371, leg. V. Litschauer, 1.10.1923 (CUP).

Results

Morphological characteristics of the twelve collections listed above fall into a bimodal distribution of two distinct species.

Septoria species A. – Figs. 1, 2.

Septoria cannabis (Lasch) Saccardo, Sylloge Fungorum 3: 557. 1884.

= *Ascochyta cannabis* Lasch, Klotzchii Herb. vivum exsic., Ed. I, no. 1509. 1846.

= *Spilosphaeria cannabis* Rabenhorst, Herbarium vivum mycologicum, Ed. II, No. 559. 1857.

= *Septoria cannabina* Westendorp, Bulletin de l'Académie Royale de Belgique Ser. II, 2(7): 576. 1857.

= *Septoria cannabis* Saccardo, nomen nudum.

?= *Rhabdospora cannabina* Fautrey, Bull. Soc. Myc. France 1899:156. 1899.

Pycnidia epiphyllous, gregarious, immersed but eventually erumpent, globose to flask shaped, averaging 90 μm in diameter, peridium thick-walled *textura angularis-globulosa*, dark brown, ostiole round, 15 μm in diameter. – Conidiogenous cells subglobose to ampulliform, simple, hyaline, holoblastic. – Conidia hyaline, straight or curved, filiform, tapering towards apex, base truncate, 3-4 septate, (30-) 42.2 (-55) x 2.0-2.5 μm .

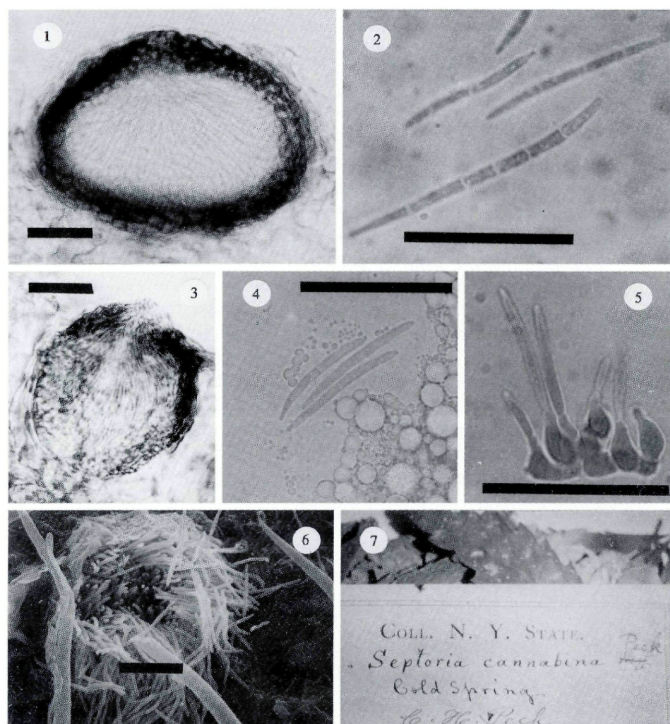
Septoria species B. – Figs. 3-7.

Septoria neocannabina McPartland, *nomen novum*.

= *Septoria cannabina* Peck, 35th Report N.Y. State Museum, Bot. p. 137, 1884; non *Septoria cannabina* Westendorp, 1857.

= *Septoria cannabis* var. *microspora* Briosi & Cavara, I Funghi Parassiti Delle Piante Coltivate Od Utili, exsiccatum no. 94. 1888.

Pycnidia epiphyllous, gregarious, immersed but eventually erumpent and nearly cupulate, globose, 66 μm in diameter, peridium thin-walled *textura angularis-globulosa*, honey-brown near the ostiole to almost colorless at the base, ostiole irregular, 20 μm in diameter. – Conidiogenous cells short ampulliform to lageniform, simple, hyaline, holoblastic, up to 8 μm long. – Conidia



Figs 1-7. *Septoria* pathogens of *Cannabis sativa*. - 1. Pycnidium of *S. cannabis*. - Conidia of *S. cannabis*. - 3. Pycnidium of *S. neocannabina*. - 4. Conidia of *S. neocannabina*. - 5. Conidiogenous cells of *S. neocannabina*. - 6. Ostiole of *S. neocannabina*. - 7. Type specimen of *S. neocannabina*. - All Figs. LM, except Fig. 8, SEM. - Bar = 25 μ m.

hyaline, usually curved, filiform, pointed at the apex with a truncate base, 1-3 septate, (20)-28.6(-30) x 1.0-2.0 μ m.

Nomenclature

Westendorp (1854) erected a new taxon in his plant disease index, '...sur les feuilles du *Canabis* [sic] *sativa*: *Septoria cannabinae* Nob. in herb.' However, he did not provide a taxonomically acceptable

description of the fungus until July 4, 1857, in *Bulletin l'Académie Royal de Belgique* Ser. II, 2(7):576. Less than 3 weeks before this, on June 19, 1857, Rabenhorst effectively published *Spilosphaeria cannabis* as exsiccatum no. 559 in *Herbarium vivum mycologicum*, Editio II.

Eleven years earlier, the fungus *Ascochyta cannabis* Lasch was released as exsiccatum no. 1509 in Rabenhorst's *Klotzchii Herbarium vivum mycologicum*, Editio I. On exsiccata labels, Lasch described the fungus in a very un-*Ascochyta* fashion, '...ascii elongatis linearibus utrinque acutis.' Saccardo (1884) transferred Lasch's taxon to *Septoria* as *S. cannabis* (Lasch) Saccardo. Lasch's basionym antedates *Sp. cannabis* Rabenhorst and *S. cannabina* Westendorp, thus Saccardo's recombination has priority. The three names represent one fungus; Rabenhorst and Westendorp's superfluous epithets are reduced to synonyms under Article 63 of the International Code of Botanical Nomenclature (ICBN) (Greuter & al., 1988). Controversy over publication dates and priority between the three taxa arises from erroneous accounts by Saccardo (1884), Seymour (1929), Oudemans (1920) and Punithalingam (1980). At least four other researchers incorrectly cite the recombined name as *S. cannabis* Saccardo, a *nomen nudum* (e.g., Szembel, 1927).

The nomenclature is also complicated by irregularities in exsiccata. Exsiccata are publications containing actual fungal specimens, rather than printed descriptions and illustrations. All exsiccata must be identical. Unfortunately, Steventon (1967) documents irregularities in Rabenhorst's series of exsiccata. Rabenhorst, a failed pharmacist, became financially dependent on sales of his exsiccata. When he ran out of certain fungi, he would substitute others under the same name. Exsiccata of *A. cannabis* Lasch and *Sp. cannabis* Rabenhorst from B contain different fungi than those deposited at BPI. The specimens deposited at B are probably originals, those at BPI represent substitutions.

Inspection of Lasch's type reveals that the specimen was collected from a plant with two diseases. A *Septoria* species and a *Phoma* species coexist on Lasch's specimen. Röder (1939) previously noted this dilemma, but accepted *Ascochyta cannabis*, rejecting *Septoria cannabis*. I disagree on three points: first, Saccardo's recombination has achieved common usage, whereas Lasch's basionym has not; second, Lasch's description (part of the taxon's protologue, see Art. 8 & 9, ICBN) agrees with *Septoria* characteristics; third, only one tiny leaf spot on the type specimen contains non-*Septoria* conidia, and these are not an *Ascochyta*, but a *Phoma* species.

Fautrey's type of *R. cannabina* is missing from PC (G. Mascarell, pers. comm.), nor is it at DI, as suggested by Dr. Mascarell (F. Bugnon, pers. comm.), nor at AUT, BPI, or FH. An exsiccatum at CUP,

Tab. 1.– Measurements of *S. cannabis* and *S. neocannabina* reported by different authors.

<i>S. cannabis</i>		<i>S. neocannabina</i>		Reference
Pycnidia (µm)	Conidia (µm)	Pycnidia (µm)	Conidia (µm)	
90	45-55 x 2.0-2.25	-	20-30	Saccardo (1884, 1892)
90	45-55 x 2.0-2.2	50-60	20-30	Kirchner (1906)
-	45-55 x 2.0-2.25	-	21-32 x 1.0-1.5	Voglino (1924)
50-(85)-90	45-55 x 2.0-2.25	-	20-30	Gitman & Boytchenko (1934)
95 (illus.)	45-60 x 2.0-2.25	-	20-30	Barloy & Pelhate (1962)
28-116	40-60 x 2.25	-	20-30 x 1.0-2.2	Ceapoiu (1958)
60-100	20-35 x 2.2	50-90	23-35 x 1.0-1.5	Savulescu & Sandu-Ville (1936)
50-130	48-57 x 2.5-3	50-80	20-30 x 1.5	Teterevnikova-Babajan (1987)
28-116	12-46 x 2-3	-	-	Watanabe & Takesawa (1936)
60-120	22-76 x 1.9-3.1	-	-	Ferri (1959)
70-120	up to 70 x 2.0-3.5	-	-	Ghani & al. (1978)
-	-	-	20-30	Peck (1884)
-	-	-	20-32 x 1.0-1.5	Briosi & Cavara (1888)

although labeled *R. cannabina*, resembles the type of *Dendrophoma marconii* Cavara (PAV!). Fautrey's description, however, closely resembles *S. cannabis*. Fautrey's taxon probably represents a later synonym, but type material needs to be located.

Nomenclature of *S. neocannabina* begins with the description of *Septoria cannabina* Peck in 1884. Papers with Peck's type indicate he originally labeled the fungus '*Septoria cannabina* Westendorp.' Later he realized his material represented a different fungus. Scratching out Westendorp's name, he wrote '*Septoria cannabina* Peck' on the herbarium label (Fig. 7). Why Peck chose an obvious homonym is a mystery. Later homonyms are rejected by Article 64 in the ICBN (Greuter & al., 1988). Since Peck's taxon is illegitimate, an avowed substitute must be provided. Peck's specimen at NYS serves as the type.

Brioso & Cavara (1888) found a fungus in Italy, noted its similarity to *S. cannabina* Peck, but decided to name it a subspecies of *S. cannabis* (Lasch) Saccardo. Exsiccata of *Septoria cannabis* var. *microspora* appear identical to Peck's specimen. I follow Voglino (1924), who previously reduced Brioso & Cavara's taxon to a synonym under Peck's name.

A '*Cylindrosporium* species' deposited at BPI also proves to be *S. neocannabina*. The specimen was collected by J.T. Rogers near Yarrow, Maryland, in 1917. Ostioles on mature pycnidia average 26 µm in diameter, oozing conidia (Fig.6). These cupulate conidiomata could easily be confused with acervuli, such as those seen in *Cylindrosporium*. Mixed with the specimen is a *Cercospora* sp., probably *C. cannabis* Hara & Fukui. Occasionally, small ovoid to fusiform conidia appear to be budding from conidia, resembling microcyclic conidiogenesis. Miller & al. (1960), Farr & al. (1989) and others list *Cannabis* as a host for *Cylindrosporium* based on this sole collection. Future lists should be amended.

Discussion

Martin (1887) synonymized Peck's taxon under *S. cannabis* (Lasch) Saccardo. Seymour (1929) and Tranzschel & al. (1933) agree. Punithalingam (1980) suggests '...the taxa are very similar and would probably be better considered as synonyms.' None of these researchers, however, indicate they examined type specimens. Many other authors consider them distinct species (e.g., Saccardo, 1884; Kirchner, 1906; Oudemans, 1920; Voglino, 1924; Gitman & Boytchenko, 1934; Savulescu & Sandu-Ville, 1936; Ceapoiu, 1958; Barloy & Pelhate, 1962; Kirchner, 1966; Teterevnikova-Babajan, 1987); again, without comparing material.

S. cannabidis and *S. neocannabina* are distinguished by several characteristics. Both species produce leaf lesions, variously described as white, yellow, ochre or gray-brown. Leaf spots may remain small and round but usually enlarge to irregularly polygonal shapes, their edges delineated by leaf veins. Spots by *S. neocannabina* exhibit a dark reddish-brown border (Peck, 1884; Kirchner, 1906; Kirchner, 1966). Pycnidia arising within leaf lesions appear either dark brown-black (*S. cannabidis*) or pale brown (*S. neocannabina*). Pycnidia form on upper surfaces of leaves, not on undersides as reported by Flachs (1936).

Microscopically, many authors have described differences between *S. cannabidis* and *S. neocannabina* (see Tab. 1). *S. cannabidis* pycnidia are large and thick-walled (Fig. 1) compared to *S. neocannabina* pycnidia (Fig. 3). Ostioles in the former fungus are relatively small, whereas *S. neocannabina* ostioles may open to nearly half the diameter of pycnidia (Fig. 6). Conidiogenesis and conidiogenous cells of both species are similar (Fig. 5). Conidia of *S. cannabidis* are longer, wider, and with more septa (Fig. 2) than those of *S. neocannabina* (Fig. 4).

Determining a distribution map for *S. cannabidis* and *S. neocannabina* is problematic. Since the two fungi can be confused, all literature is suspect. Voucher specimens must be reexamined. This work has begun and will be presented in a future publication.

Acknowledgments

Curators of B, BPI, BR, CUP, MICH, NYS and PAV are thanked for lending collections; F. A. Uecker supplied figure five; D. F. Farr provided a pre-submission review. This work was partially funded by a grant from Hortapharm, B.V., The Netherlands.

References

- Barloy, J. & J. Pelhate (1962). Premières observations phytopathologiques relatives aux cultures de chanvre en Anjou. – Ann. Epiphyties 13: 117–149.
- Briosi, G. & F. Cavara (1888). *Septoria cannabidis* var. *microspora*. – I Funghi Parassiti Delle Piante Coltivate Od Utili, exsiccatum no. 94.
- Ceapoiu, N. (1958). *Cinepa*, Studiu monografic. – Editura Academiei Republicii Populare Romine, Bucharest, 652 pp.
- Constantinescu, O. (1984). Taxonomic revision of *Septoria*-like fungi parasitic on Betulaceae. – Trans. Br. mycol. Soc. 83: 383–398.
- Farr, D. F. (1991). *Septoria* species on *Cornus*. – Mycologia 83: 611–623.
- (1992a). Species of *Septoria* on the Fabaceae, subfamily Fabioideae, tribe Genisteae. – Sydowia 44: 13–31.
- (1992b). Species of *Septoria* on orchids. – Mycological Society of America Newsletter 43(1): 31.
- , G. F. Bills, G. P. Chamuris & A. Y. Rossman (1989). Fungi on plants and plant products in the United States. – APS Press, St. Paul, MN, 1252 pp.

- Flachs, K. (1936). Krankheiten und Schädlinge unserer Gespinstpflanzen. – Nachrichten über Schädlingsbekämpfung 11: 6–28.
- Gamalitskaia, N. A. (1964). Micromycetes of the Southwestern part of the Central Tien Shan Mountains. – Akad. Nauk Kirghiz S.S.R., 175 pp.
- Ghani, M., A. Basit & M. Anwar (1978). Final Report: Investigations on the natural enemies of marijuana, *Cannabis sativa* L. and opium poppy, *Papaver somniferum* L. – Commonwealth Institute of Biological Control, Pakistan station. 26 pp. + 12 illus.
- Gitman, L. & E. Boytchenko (1934). 'Cannabis' pp.45–53 in: A manual of the diseases of the new bast-fibre plants. – Inst. New Bast Raw Materials, Moscow, 124 pp.
- Greuter, W. & al. (1988). International Code of Botanical Nomenclature, 14th International Botanical Congress, Berlin. – Koeltz Scientific Books, Königstein, 328 pp.
- Kirchner, H. A. (1966). Phytopathologie und Pflanzenschutz. Vol. 2. – Akademie Verlag, Berlin, 617 pp.
- Kirchner, O. (1906). 'Hanf, *Cannabis sativa* L.' – pp. 319–323. In: Die Krankheiten und Beschädigungen unserer landwirtschaftlichen Kulturpflanzen. – E. Ulmer, Stuttgart, 637 pp.
- Martin, E. (1887). Enumeration and description of the Septorias of North America. – J. Mycol. 3: 37–41.
- McPartland, J.M. (1991). Common names for diseases of *Cannabis sativa* L. – Plant Disease 75: 226–227.
- (1992). C.H. Persoon: a phanerogamic footnote. – Mycotaxon 45: 257–258.
- Miller, P. R., F. Weiss & M. J. O'Brien (1960). Index of Plant Diseases in the United States. – Agriculture Handbook No. 165. U.S.D.A., Washington, D.C., 531 pp.
- Mushtaque, M., G. M. Baloch & M. A. Ghani (1973). Natural enemies of *Papaver* spp. and *Cannabis sativa*. – Annual report, Commonwealth Institute of Biological Control, Pakistan station, pp. 54–55.
- Oudemans, C. A. J. A. (1920). Enumeratio Systematica Fungorum II: 945–947. – Comitum, The Hague.
- Peck, C. (1884). *Septoria cannabina*. – 35th Report N.Y. State Museum, Bot., p. 137.
- Punithalingam, E. (1980). *Septoria cannabis*. – CMI Descriptions of Pathogenic Fungi and Bacteria No. 668.
- & B. E. J. Wheeler (1965). *Septoria* spp. occurring on species of *Chrysanthemum*. – Trans. Br. mycol. Soc. 48: 423–439.
- Rataj, K. (1957). Skodliví cinitele pradných rostlin. – Prameny literatury 2: 1–123.
- Röder, K. (1939). Über einen neuen Hanfschädiger, *Didymella arcuata* n. sp. und seine Nebenfruchtformen. – Phytopathol. Z. 12: 321–333.
- Saccardo, P. A. (1884). *Septoria cannabis*. – Sylloge Fungorum 3: 557.
- (1892). *Septoria cannabina*. – Sylloge Fungorum 10: 381.
- Savulescu T. & Sandu-Ville C. (1936). Beitrag zur Kenntnis der Micromyceten Rumäniens. – Hedwigia 75: 159–233.
- Schultes, R. E., W. M. Klein, T. Plowman, & T. E. Lockwood (1974). *Cannabis*: an example of taxonomic neglect. – Bot. Mus. Leaflet. Harv. Univ. 23: 337–367.
- Seymour, A. B. (1929). Host Index of the Fungi of North America. – Harvard University Press, Cambridge, MA, 732 pp.
- Small, E. & A. Cronquist (1976). A practical and natural taxonomy for *Cannabis*. – Taxon 25: 405–435.
- Steventon, J. A. (1967). Rabenhorst and fungi exsiccati. – Taxon 16: 112–119.
- Sutton, B. C. (1980). The Coelomycetes – Fungi imperfecti with pycnidia, acervuli, and stromata. – Commonwealth Agricultural Bureau Publications, London, 696 pp.
- & I. G. Pascoe (1987). *Septoria* species on *Acacia*. – Trans. Br. mycol. Soc. 89: 521–532.

- Szembel, S. J. (1927). A new species of rust on hemp. – *Commentarii Instituti Astrachanensis ad defensionem plantarum*, i(5-6): 59-60.
- Teterevnikova-Babajan, D. (1987). Griby roda *Septoria* v SSSR. – *Akademia Nauk Armjanskoi SSR, Erevan*, 478 pp.
- Tranzschel, V., L. Gutner & M. Khokhryakov (1933). A list of fungi found on new cultivated textile plants. – *Moscow Inst. Nov. Lubian. Syr'ia, Trudy* 4: 127-140.
- Voglino, P. (1924). *Patologia Vegetale*. – *Unione Tipografica-Editrice Torinese, Torino*, 287 pp.
- Watanabe, T. & M. Takesawa (1936). Studies on the leaf-spot disease of the hemp. – *Ann. Phytopath. Soc. Japan* 6: 30-47.
- Westendorp, G. D. (1854). *Les Cryptogames*. I.S. Van Doosselaere. Gand, Belgium. 301 pp.

(*Manuscript accepted 23rd August 1994*)

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Sydowia](#)

Jahr/Year: 1995

Band/Volume: [47](#)

Autor(en)/Author(s): McPartland John M.

Artikel/Article: [Cannabis pathogens XI: Septoria spp. on Cannabis sativa, sensu stricto. 44-53](#)