

Zizania latifolia and *Ustilago esculenta*, a Grass-Fungus Association¹

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Zizania latifolia (Manchurian wild rice), native to eastern Asia, is often infected by the smut fungus, *Ustilago esculenta*, causing culm enlargement and failure to produce flowers. The enlarged infected culms have been used as a vegetable (gau sun) in China since the 10th century. The occasionally-used name *Z. caduciflora* is shown to be only a synonym. To facilitate identification of the host, a taxonomic key shows that *Z. latifolia* differs from and is fully distinct from the American species of *Zizania*. The nature and structure of the fungus and the history and cultivation of the vegetable are described. As a precaution we propose quarantine of the host and fungus to prevent possible disastrous widespread infection of American wild rices by the fungus.

Zizania latifolia (Griseb.) Turcz. ex Stapf (Manchurian wild rice, Manchurian water rice, Manchurian ricegrass, broad-leaved wild rice or zizania, Asian or Chinese or Far-Eastern wild rice) is a perennial aquatic grass native to eastern Asia (Fig. 1, 2). In southern China and Taiwan it is usually parasitized by a smut fungus, *Ustilago esculenta* Hennings, which stimulates enlargement of the culms of the grass. For several centuries the swollen, infected culms have been eaten by the Chinese as a vegetable, commonly called *gau sun* or *kah peh sung*. The presence of the fungus suppresses flowering of the host, as observed in Taiwan and Japan by one of us (LRB); see also Roger, 1951, and Thrower and Chan, 1980. We have not determined positively whether *U. esculenta* infects the American species of wild rice, because references in the literature to *Z. aquatica* L. are not accompanied by voucher specimens and may be based on misidentifications. Furthermore, *Z. latifolia* and *Z. aquatica* sometimes were lumped as one species in the older literature.

The American wild rices (primarily *Z. aquatica* L. and *Z. palustris* L.) are important constituents of aquatic plant communities and food for coot (*Fulica americana* L.), snow geese (*Chen hyperborea* Pallas), 2 kinds of rails, 6 of song birds, and 13 of ducks (Martin and Uhler, 1939; Martin et al., 1951). *Zizania palustris* is a well-known source of edible grains and is becoming a new cultivated crop of some significance in Minnesota. Because infection of American wild rices, near relatives of *Z. latifolia*, by *U. esculenta* might suppress flowering and, therefore, be devastating to seed production, we recommend that immediate steps be taken to prevent the entry into North America of the host with its perennial, systemic fungus. To this end we have communicated our concern to the Animal and Plant Health Inspection Service (APHIS), an arm of the United States Department of Agriculture responsible for the interception of harmful organisms. (We pointed out previously the need for quarantine; Batra et al., 1978, pp. 285–

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Fig. 1-2. Fig. 1. *Zizania latifolia* in shallow water, Snowden Pond, Patuxent Wildlife Research Center, near Laurel, Maryland, autumn 1974. Plants ca 2 m tall. Inflorescence at upper center. Introduced from Asia. Fig. 2. *Zizania latifolia*, showing rhizomes and uninfected culms as grown in pots in greenhouse at Beltsville, Maryland, in 1976. Source as in Fig. 1.

286.) It is desirable also that the danger accompanying accidental introduction of the fungus be made known to commercial institutions responsible for its importation into North America. We present here a general account of both the grass and its fungus, their distribution, vernacular names, and methods of timely identification to facilitate proper disposition of living infected plants.

Several papers have dealt exclusively or largely with *Z. latifolia* and its use as a vegetable. The first 2 papers did not recognize the presence of a fungus associated with the vegetable. Hance (1872) treated *Z. latifolia* under the name *Hydropyrum latifolium* Grisebach and gave a firsthand account of the vegetable as used in China, followed by astute observations on the morphology and taxonomic relationships of the grass. Stapf (1909) provided important information on nomenclature, taxonomy, morphology, cultivation, and uses. Camus (1922) gave a brief account, and later (1950) a much amplified, illustrated discussion of these same features for both *Z. latifolia* and *Z. aquatica*. Thrower and Chan in this journal (1980) discussed the vegetable, its cultivation, and aspects of the fungus. Chan and Thrower (1980a,b,c,d) carried out detailed studies of the general chemistry of host-parasite interaction, including carbohydrate metabolism and the actions of growth substances. The papers just cited contain many references to various aspects of the host and the vegetable and its fungus; consequently, it is not our intent here to provide a complete summary of all of the literature. Also, it is not our intent here to deal with the morphology, ecology, hybridization, cultivation, etc., of *Z. latifolia* per se, although we found a number of Russian papers on these subjects.

THE VEGETABLE GAU SUN

Grains of *Z. latifolia* have been used for food, sometimes in the form of flour, and the grains and rhizomes have been used as diuretics and as medicines for anemia, heart disease, and liver disease (Stapf, 1909; Camus, 1950). In Europe the plants have been used for forage and to make paper (Camus, 1950). In New Zealand the species is a troublesome weed which is not eaten by livestock (Cumberland, 1966).

Ancient Chinese herbals and encyclopedias refer to the cultivation of *Z. latifolia* as a vegetable back at least to the 10th century (Stapf, 1909; Camus, 1950). *Zizania latifolia* was also used as a grain in ancient times, but later came to be used primarily as a vegetable. Grain of *Z. latifolia* was used in rituals of the Chou dynasty according to *Chou li* (written about 1100 B.C.) or Ritual of the Chou Dynasty (also mentioned by Huang, 1978). A recent book (Chang, 1977) concerning foods in Chinese culture includes (p. 32) a poem dating back to the Chou dynasty (12th century B.C.—221 B.C.) which refers to "corn of zizania." In this case, corn means the *Zizania* grains. In Europe Osbeck (1757), a Swede and a pupil of Linnaeus, gave one of the earliest accounts of the use by the Chinese of the plant as a vegetable.

At present only the succulent culms and rhizomes infected with *U. esculenta* are propagated and highly prized as *gau sun* (Leu et al., 1977; Thrower and Chan, 1980). Some names for the young shoots used as vegetables are: *gau sun*, *kau sun*, *jiao sun* or *chiao sun* (literally, cane shoots)—Canton; *chiao pai*, *co ba*—Shanghai; *chiao qua*, *kiao pai tsai*, *kiao sun*—Peking; *kah peh sung*—Taiwan; *makomo*—Japan; *makomu*—Okinawa; *cu nieng*, *cay lua mieu*—Indo-China.

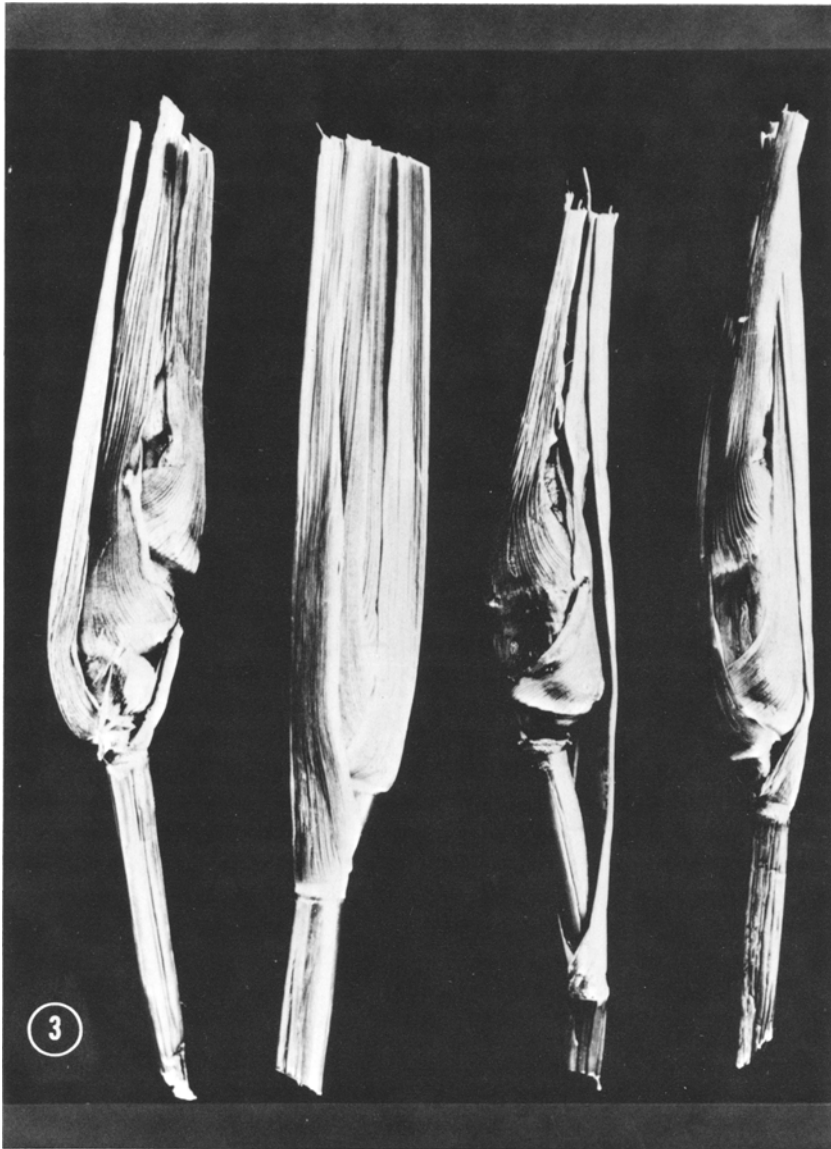


Fig. 3. *Gau sun* or galls of *Ustilago esculenta* in *Zizania latifolia* (ca nat. size).

Gau sun resembles small unhusked ears of corn (maize) (Fig. 3), but with an attenuated and curved apex, and, when outer leaves are removed, looks like a parsnip upside down. Botanically, the vegetable consists of a series of sheathing leaves just below the meristem. The internodes are so close that the entire shoot is a conical to fusiform, succulent, rather compact, fleshy gall. It contains mycelium and chlamydospores in various stages of development. Borne in clusters, these shoots are usually 10–15 cm long, 2–4 cm thick at widest point. The swelling is caused by the excessive activity of the apical and axillary meristems. The fungus is perennial in the rhizomes.



Fig. 4. *Gau sun* as marketed in a Chinese vegetable store.

According to Yang and Leu (1978) in Taiwan there are 3 cultivars of *kah peh sung* with green, white and red "outer skin of the gall." Stools are planted in late December, each with 2–3 stalks. The fields are kept flooded until the following October or early November when each clump has 20–30 stalks with galls, each including usually 3, sometimes 4 nodes below the meristem. Yang and Leu (1978) state that, "The green cultivar forms galls from April to November in the Puli area; for red and white cultivars, *Z. latifolia* is planted later and the galls are harvested in October." These late plantings have smaller galls. Additional information on cultivation is provided by Huang (1978) and Thrower and Chan (1980). The latter distinguish 2 cultivars sold in the Hong Kong market: The one from Canton is oval in cross section and has a rather soft texture; the other, from Shanghai, is round and firm, almost tough. We could not substantiate these findings on the basis of specimens examined at the National Fungus Collections, Beltsville.

Gau sun is used as a late spring, summer and fall vegetable. Before marketing outer green leaves are removed and discarded, much like cornhusks (Fig. 4); the inner white core is parboiled whole or sliced, and sautéed with meats and other vegetables. It is also sold in cans and fresh-frozen. Texture of the uncooked vegetable purchased in Taiwan resembled fresh bamboo shoots; sautéed or parboiled it had a nutty flavor somewhat akin to coconut (observations by Batra). During early fall, at least in Japan, affected plants retain their green color, in contrast to yellow, uninfected plants (Hori, 1907). Plants experimentally disinfected with hot water produce normal spikes whereas the infected ones do not do so (Ou, 1938).

In Japan the fungus was at one time sold in drug stores as *makomo-zumi* or *makomono-nezumi* meaning zizania charcoal or zizania root charcoal, respectively. "The olive brown powdery spores are used by women having thin eyebrows to make them look heavier by painting the spores over them. When mixed in an oil, they are smeared on the scalp and hair by older women having thin or grey hairs" (Miyabe, 1895). The spores were also used in lacquer by mixing them with lac (Kawagoe, 1924).

DISTRIBUTION, NOMENCLATURE AND RECOGNITION OF ZIZANIA

Zizania has been placed in the subtribe Zizaniinae of the tribe Oryzeae (Terrell and Robinson, 1974). In addition to the Asian *Z. latifolia*, there are 3 North American species of *Zizania* (following Dore, 1969). Southern wild rice (*Z. aquatica*) occurs on the Atlantic Coastal Plain from northeastern North America to central Florida, extending inland to the upper midwestern United States and Louisiana. Northern wild rice (*Z. palustris*) ranges from northeastern North America west across the Great Lakes region to southcentral Canada. Texas wild rice (*Z. texana* Hitchcock) is an endangered species in a very local area in Hays County, Texas (Terrell et al., 1978).

Distribution of *Z. latifolia* is rather widespread in eastern Asia, but it may have been introduced in southeastern Asia and parts of China and the USSR. In the USSR it is indigenous in the Dahuria region of eastern Siberia and in the Udsu, Ussuri, and Zeya-Bureya regions in the Soviet Far East (Komarov, 1936; Tzvelev, 1976); these regions are north of Manchuria and Mongolia. It is introduced in western USSR. Kopylova (1961) and Shaga and Shaga (1972) provide more detailed geographical and ecological information for the USSR and for other countries. In China it is in Manchuria and several provinces, often introduced for cultivation (Thrower and Chan, 1980). Li (1970) noted that *Z. latifolia* is "distributed south to Taiwan and north to Harbin and is especially cultivated in the marshy regions south of the Yangtze valley." Also, it occurs in Japan, Okinawa, Korea, Taiwan, northeast India, Burma, Malaya, Viet Nam or Indo-China (*sensu lato*) and has been introduced in Europe, New Zealand, and rarely in North America (see below). Recorded natural habitats, at least for the USSR, include borders of lakes, still-water bays, and slow-running streams (Komarov, 1936).

Zizania latifolia was erroneously combined with *Z. aquatica* by some older writers and is used interchangeably by some authors (e.g., Chang, 1977). In addition, an incorrect name, *Z. caduciflora* [Trinius] Handel-Mazetti, has occasionally been used as correct (e.g., Thrower and Chan, 1980, Chan and Thrower, 1980a,b,c,d). Some mycological papers such as Sawada (1916) and Su (1961) identify it as "*Z. aquatica*" but do not describe the host well or refer to an authoritative monograph to ascertain the identity of the host investigated or provide voucher specimens. As a matter of usage, it is worth pointing out that several authoritative taxonomic publications have correctly used the name *Z. latifolia* and at the same time considered it a fully distinct species: Stapf, 1909; Fassett, 1924 in a revision of *Zizania*; Camus, 1950; Dore, 1969; and Tzvelev, 1976, in a grass flora of the USSR. In addition, the name and authorities appear correctly in *Index Kewensis* and in Zander's handbook (Encke and Buchheim, 1972).

Hoping to lay the name *Z. caduciflora* to rest as nothing more than a synonym

of *Z. latifolia*, we provide a résumé of the nomenclature, with comments based on our research. The following lists the correct names followed by pertinent synonymy (publication dates from Stafleu, 1967).

Zizania latifolia (Grisebach) Turczaninow ex Stapf, Kew Bull. 1909: 385–386. 1909. (This may be correctly cited also as *Z. latifolia* (Grisebach) Stapf, omitting the proposing author, following the recommendation of ICBN Art. 46, Rec. 46C (Stafleu et al., 1978).

Synonyms:

Z. latifolia Turczaninow, Bull. Soc. Nat. Mosc. 1: 105. 1838. (nomen nudum).

Limnochloa caduciflora Turczaninow ex Trinius, Mem. Acad. Sci. St. Petersb. ser. 6, 5, 2: 185. 1840. (as synonym).

Hydropyrum latifolium Grisebach, in Ledebour, Flora Rossica 4: 466. June 1853.

Z. dahurica Turczaninow ex Steudel, Synopsis Plantarum Glumacearum 1: 4. December 1853.

Z. caduciflora (Trinius) Handel-Mazzetti, Symb. Sin. 7: 1278. 1936. Nom. Illeg. (superfl.) incl. type of *Hydropyrum latifolium* Griseb. (1853).

Portions or all of the above synonymy have been listed or discussed by Stapf (1909), Fassett (1924), Camus (1950), and Afanassiev (1960). Afanassiev correctly emphasized that *Limnochloa caduciflora* is a synonym of *Z. latifolia*. Turczaninow (1838) published the name *Z. latifolia* without a description, thus the name is not valid (Article 32, ICBN). In 1840 *Limnochloa caduciflora* was described by Trinius, using a genus name in the Cyperaceae. An examination of the format (including the width of printed lines) and typography of the Trinius publication shows that *Limnochloa caduciflora*, although accompanied by a description, was published as a synonym of *Hydropyrum esculentum* Link, which in turn was based on the American species *Z. palustris* L.; thus *Limnochloa caduciflora* is nomenclaturally not valid according to Art. 34, ICBN. Following this publication, Grisebach (in Ledebour, 1853) validly published *Hydropyrum latifolium*. In December 1853, Steudel published a new name, *Z. dahurica*, but Grisebach's name has priority. Stapf (1909) transferred Grisebach's name to *Zizania*. Handel-Mazzetti's (1936) binomial was based on an invalid name, as indicated above and its priority dates from 1936. The binomial is superfluous (illegitimate) since the author included *Hydropyrum latifolium* Griseb. in synonymy, of which the epithet should have been adopted.

Morphological comparisons of *Z. latifolia* with the North American wild rices were provided by Hance (1872), Stapf (1909), Fassett (1924), and Camus (1950). Most of the characteristics they mentioned were confirmed in the present study as diagnostic for separating species. The following key uses some of the more easily observed characteristics and at the same time is intended to point out the important and distinct characters of *Z. latifolia*. In the key we include the North American species as one entity contrasting with *Z. latifolia* in order to simplify the key for our purpose. A table comparing the 3 American species is provided elsewhere (Terrell et al., 1978). They may differ in chromosome number and karyotype; new data and a review of earlier data were provided by Huang (1978).

Key for identification of *Z. latifolia*

- A. Rhizomes (Fig. 2) present, plants perennial; branches of inflorescence, at least the middle ones, bearing both pistillate and staminate spikelets on the same branch; cupules (expanded ends) of pedicels of pistillate spikelets ciliolate and only slightly wider (ca 0.3–0.6 mm wide) than cupules of the staminate spikelets (ca. 0.2–0.5 mm wide); staminate spikelets usually with awns to 6 (to ca 10) mm long *Z. latifolia*
- AA. Rhizomes absent, plants annual, or *Z. texana* perennial with very short rhizomes or none; inflorescence branches bearing pistillate spikelets on upper branches only and staminate spikelets on lower branches only; cupules of pistillate spikelets glabrate and 2 or 3 times wider (ca 0.5–1.2 mm) than cupules of the staminate spikelets (ca 0.2–0.6 mm wide); staminate spikelets usually without awns or awns to 2 mm long *Z. aquatica*, *Z. palustris*, *Z. texana*

The differences included in the key are not the only ones which differentiate these species (Terrell and Wergin, 1981), but they are easier to observe and

describe than some of the other differences. It is usually necessary to have inflorescences to distinguish the species of *Zizania*. We do not know any way of distinguishing the species on the basis of culm sections, which often are the only portion of the plant provided for vouchers of infection by *Ustilago esculenta*. Specimens preserved at our center consisted of culm pieces, were variously labelled either *Z. latifolia* or *Z. aquatica*, and cannot be identified to species. Ligule morphology may differ among the species, but this character needs further study.

CULTURE OF *Z. LATIFOLIA* IN THE UNITED STATES

Zizania latifolia has been introduced into the United States approximately 11 times (USDA Plant Inventory records). The only surviving introductions are the plants growing in shallow water in Snowden Pond at the Patuxent Wildlife Research Center of the U.S. Department of the Interior near Laurel, Maryland (Fig. 1). This accession was established in the 1920s after being introduced under the aegis of C. E. Chambliss, U.S.D.A. scientist, from an unknown source and locality in Asia (Dore, 1969, p. 21). The plants have been shifted from one locality to another within the Center, and have suffered the vicissitudes of being partly eaten by muskrats (*Ondatra zibethica* L.), Canada geese (*Branta canadensis* L.), and deer (*Odocoileus virginianus* L.) (F. M. Uhler, pers. comm.). The present population of fewer than 20 plants has been observed for several years by Terrell. There have never been any culm enlargements and there is every indication that the Patuxent plants are free of *Ustilago esculenta*. One or a few plants may produce inflorescences (Fig. 1) in September or October, but the pistillate spikelets usually are killed by frost in late October before they can produce mature caryopses. A few plants transplanted to a greenhouse at Beltsville, Maryland, flowered rarely, but produced a few "seeds" by self-pollination. Plants from the Patuxent population were sent to W. H. P. Emery, Department of Biology, Southwest Texas State University, San Marcos, Texas, and later Emery sent plants to James Percich and R. L. Bowden, Department of Plant Pathology, University of Minnesota, St. Paul. Accordingly, there are 3 known plantings now in the United States.

Dore (1969) stated that plants of *Z. latifolia* from Japan were established in a botanic garden and greenhouse at the Plant Research Institute, Agriculture Canada, Ottawa, Ontario, where it has never flowered. Stapf (1909) noted that plants grown at Kew, England, never flowered. W. H. P. Emery reported (pers. comm.) that the plants in Texas have flowered regularly and have produced viable caryopses, from which new plants have grown. Ovesnov and Aristova (1966), among others, described results of experiments on seed viability and dormancy.

THE FUNGUS—*USTILAGO ESCULENTA*

The fungal nature of *gau-sun* was recognized in the Chou Dynasty encyclopedia *Raya* (ca 400 B.C.), the word *chu-su* or *ku-su* meaning the green plant *Zizania latifolia* and the fungus. Hennings (1895) named the latter *Ustilago esculenta* and correctly determined its host, but apparently mistook the swollen shoots, obtained in Hanoi market, as "floral stalk." Miyabe (1895) briefly noted its structure and commented on its use in Japan, and Hori (1907) observed spore germination in vitro and concluded that the fresh smutted shoots from Japan

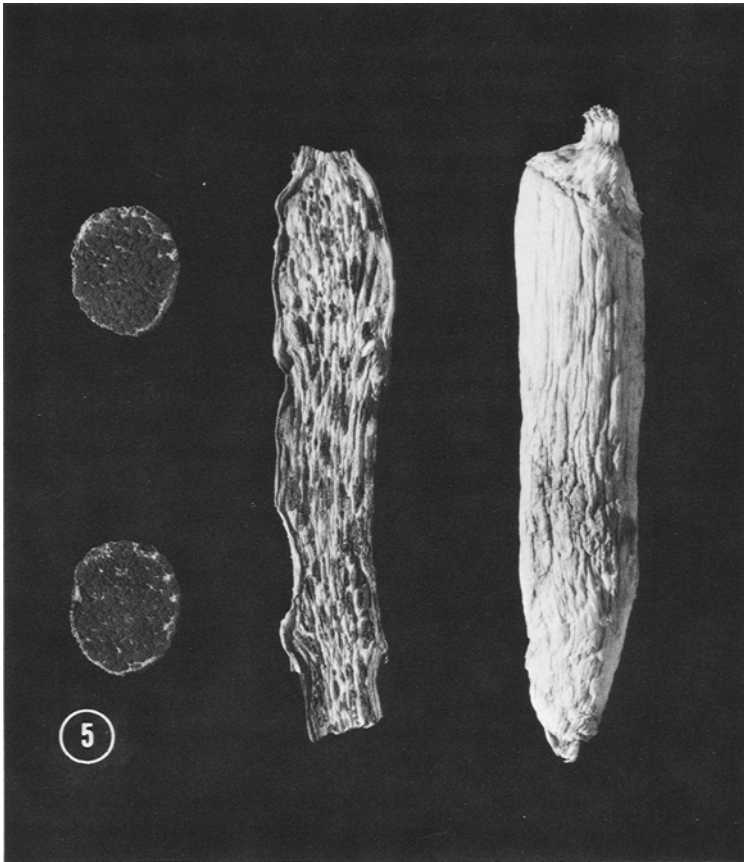


Fig. 5. External view, longitudinal and cross sections showing fungus sori in *gau sun* (ca nat. size).

were 2–4 times smaller than the dried specimens from Taiwan. F. W. Patterson (1912) of the U.S.D.A. Mycology Laboratory, published an abstract on *U. esculenta* as it appeared on *Zizania latifolia*, reared in greenhouses of the Department, but brought from Canton between 1908–1911.

Sawada (1916) compared *U. esculenta* infection on *Z. latifolia* with that on "*Z. aquatica*." Su (1961) and Yang and Leu (1978, 1980) investigated the histopathology of galls and germination of spores leading to the formation of promycelium and sporidia. The latter authors recognize 2 "strains": (1) teliospore (T) strain, characterized by the formation of sori during the initial stages of the gall formation and with longitudinal streaks visible from outside. "The gall and the sori induced by the T strain are shorter and wider than those by the M-T strain" (Yang and Leu, 1978); (2) the "mycelia-teliospore (M-T)" strain forms sori in the later stages of gall formation and the galls are without streaks. We could not differentiate these strains based on herbarium specimens we examined.

The ellipsoid to spindle-shaped sori are borne throughout the swollen shoots in lysigenous yellow cavities within the white flesh (Fig. 5). As the teliospores mature, the dusty or powdery sori turn black but remain usually confined by

patches of host flesh (Fig. 5, middle). They abstrict from closely septate hyphae. They are globose to subglobose, rarely ellipsoid, reddish-brown, 6–12 μm in diameter and with minute echinulations or punctations. Upon germination, teliospores form a septate, hyaline to pale yellow promycelium that bears abundant terminal or lateral, fusiform sporidia 30–40 \times 2–3 μm .

Yang and Leu (1978) obtained slimy, whitish-yellow pure colonies from infected tissues. These colonies turned brown and bore masses of sporidia in 10–20 days at 20°C. We also readily cultured the fungus from Taiwanese specimens on potato dextrose agar and confirmed their findings, as do Chan and Thrower (1980b). *Ustilago esculenta* is a hardy fungus and can withstand environments with amplitudes comparable to those of North America. It can withstand –15°C and in fact chilling enhances teliospore spore germination. Ou (1938) apparently obtained fungus-free plants when he immersed infected material in water at 52°C for 30 min, but both the plant and the fungus died at 54°C held for 15 min. At 48°C there was no germination of teliospores held in a water bath for 50 min.

Ustilago esculenta, discussed as *Melanopsichium esculentum* (P. Henn.) Mundkur and Thirumalachar (1952), should not be confused with the general leaf smut *Entyloma lineatum* (Cke.) J. J. Davis (= *Ustilago lineata* Cke.) of American wild rice *Z. aquatica* and *Z. palustris*, the latter treated as *Z. aquatica* var *angustifolia* Hitchcock in older mycological literature. It causes leaf or culm spots only, without any hypertrophy. The sori with teliospores are lead-colored to brownish-black, short to long linear. The teliospores are yellowish-brown, subglobose to polyhedral, 6–10 μm and smooth. *Ustilago esculenta* is also readily distinguishable from *U. scitaminea* Sydow on sugarcane: the latter has long, whiplike infected shoots and centripetal maturity of spores in the sori.

Specimens examined at National Fungus Collection, Beltsville (BPI)

CHINA: Peking: Hopei, on *Z. latifolia*, 17.X.1930, K. L. Teng, 1521; Changsha, 7.X.1919, O. F. Cook; Chekiang: Hsiang-shan-hsien, probably on *Z. latifolia* XII.1935, S. H. Ou, 172: One interception at San Francisco in 1972, probably on *Z. latifolia*, loc. unknown. Kiangsu: Taihoku, on "*Z. aquatica*," 17.XI.1933, Y. Hashioka. INDIA: Manipur: Impal. On *Z. latifolia*, Exsic. LIII, Indian Ustilaginales by B. B. Mundkur, coll. VIII.1940, G. I. Gimson. JAPAN: Tokyo, on *Z. latifolia*, sent by H. Hori in 1908; Wakagama Kii, "*Z. aquatica*," no dates, coll. T. Yamamoto; 3 interceptions, one at Philadelphia in 1948, two at New York in 1936 and 1949 respectively, all three probably on *Z. latifolia*. TAIWAN: Taipei, on *Z. latifolia*, 2.XI.1927, K. Sawada (Fig. 5). UNITED STATES: on *Z. latifolia*: Washington, D.C. 15.XI.1911, C. S. Scofield, U.S.D.A. greenhouse; Taichung, 4.V.1981, *Batra* 3931. VIETNAM: Tonkin, no date (*Batra* 3527).

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Book Review

Morphology and Infrageneric Relationships in the Genus *Jatropha* (Euphorbiaceae). Bijan Dehagan and Grady L. Webster. 73 pp. 33 pls. University of California Publications in Botany, vol. 74. University of California Press, Berkeley, 1979. \$10.50.

This biosystematic study of supraspecific taxa in *Jatropha* is the product of Dehagan's 10 years of research on the genus and Webster's broad knowledge of the family. They here provide a major contribution to the understanding of this large (165–175 known species) and complex group.

In spite of the apparent naturalness of *Jatropha* and its uniformity in a number of morphological and cytological characters, the genus is remarkably diverse. Habit varies from facultatively annual to herbaceous perennial to various kinds of trees and shrubs. Variation in leaves, inflorescences, flowers, and types of pollination is also extensive. The variation in habit, inflorescence, and floral characters follows two evolutionary trends in the two subgenera.

This work includes detailed studies of all aspects of morphology and summarizes what is known about pollination and chromosome numbers in *Jatropha*. This breadth has produced discoveries of general biological interest: floral morphology of some taxa suggests ant pollination; the shift from self-pollination to outcrossing in *Jatropha* reverses the usual direction in angiosperms; the cotyledons remain within the seed in the germination of the seeds of some species; and doubling the size but not the number of chromosomes of *J. cardiophylla* makes it genetically equivalent to a polyploid.

Keys to the 2 subgenera, 10 sections, and 10 subsections, a checklist of all names at or above the varietal rank with literature citations and type localities, and a wealth of photographs of morphological variation round out this superb study.