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Domestication of Sawa Millet (*Echinochloa colona*)[1]

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Two species of Echinochloa *are grown as cereals.* Echinochloa crusgalli *is native to temperate Eurasia and was domesticated in Japan some 4,000 yr ago.* Echinochloa colona *is widely distributed in the tropics and subtropics of the Old World. It was domesticated in India.* Echinochloa colona *is morphologically allied to* E. crusgalli, *but hybrids between them are sterile.* Echinochloa colona *differs consistently from* E. crusgalli *in having smaller spikelets with membranaceous rather than chartaceous glumes. Hybrids between wild and cultivated taxa of* E. colona *and between those of* E. crusgalli *are fertile. Cultivated* E. colona *is variable. It is grown as a cereal across India, Kashmir and Sikkim. Four morphological races are recognized, although these do not have geographical, ecological or ethnological unity. Race laxa is confined to Sikkim where races robusta, intermedia and stolonifera are also grown. In India, races robusta, intermedia and stolonifera are often grown as mixtures, and* Echinochloa *is sometimes grown as a mixture with other cereals, particularly* Setaria italica *(foxtail millet) or* Eleusine coracana *(finger millet). The species is planted on poor soil, and some cultivars mature in less than 2 mo. They hold considerable promise as cereals for the semiarid tropics.*

The genus *Echinochloa* (Gramineae) includes some 20 species that are distributed widely in the warmer parts of the world. Several species are aggressive colonizers of disturbed habitats, and 2 are cultivated as cereals. The most aggressive weed is *E. oryzoides* (Ard.) Fritsch. This species is also recognized taxonomically as *E. crusgalli* var. *oryzicola* (Vasinger) Ohwi. It differs from *E. crusgalli* (L.) Beauv. in having $2n = 36$ rather than $2n = 54$ chromosomes. Yabuno (1962, 1966) indicates that *E. crusgalli* has one genome in common with *E. oryzoides*. The latter species is a weed of paddy rice. It is Asian in origin but accompanied rice as a weed to Africa, Australia and the Americas. The weed resembles rice in vegetative traits and is difficult to weed out during early growth. It comes into flower a few days earlier than the rice cultivar it grows with, and it disperses seeds before the rice crop is harvested. This insures a new population of weeds when rice is planted again in the same field. In the Caucasus of Russia a race of *E. oryzoides,* known as *E. macrocarpa* Vasinger, lacks the ability of efficient natural seed dispersal (Rozhevits, 1937) and is harvested as a crop. Seeds escaping the harvester, or included with the rice harvest, insure new weed populations in successive generations. Grains of *E. oryzoides* are used in the Caucasus for distillation of alcohol and for grinding into flour from which flat cakes are baked. Rozhevits (1934) indicates that the market value of this weed almost equals that of barley (*Hordeum vulgare* L.).

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Barnyard grass (*E. crusgalli*) is a common weed of temperate regions of both the Old and New Worlds. This species is extensively cultivated in Japan, Korea and northern China. Hjelmqvist (1969) suggests that *E. crusgalli* was cultivated in Sweden during the late Bronze Age when the climate of northern Europe was warmer than it is today. Archaeological evidence suggests that it was grown in Japan as early as the Yayoi period, dating back some 4–5 millenia (Watanabe, 1970).

Echinochloa colona (L.) Link is a more tropical species than *E. crusgalli*. It is sown in the Central African Republic (Tisserant, 1953) where the grains are fermented to make beer. Stuhlmann (1909) mentions that *E. colona (Panicum colonum* L.) is grown as a cereal in the Ruvuma district of Tanzania where it is known as *chindumba*. It is harvested as a wild cereal in Malawi (de Wet, 1977). This species was also harvested, or perhaps grown as a cereal, in predynastic Egypt. Intestinal contents of mummies excavated at Naga ed-Der include, among other plant remains, recognizable grains of *E. colona* (Dixon, 1969). It is widely grown today only in tropical India, where *E. colona* probably is a relatively recent domesticate. No archaeological remains of *E. colona* have been identified among plant remains of the numerous early farming sites so far excavated in India (Vishnu-Mittre, 1977). In southern India, *E. colona* often invades cultivated fields as a weed and is harvested as a wild cereal (Fischer, 1934). Where it is grown as a cereal in southern India, the species is often planted as a mixture with *Eleusine coracana* (L.) Gaertn., or with *Setaria italica* (L.) Beauv. The cultivated complex of *E. colona* is variable and several races are recognized by farmers. In contrast, *Paspalum scrobiculatum* L. (*kodo*), another indigenous millet from tropical India, is known in the archaeological record dating back some 3,000 yr (Kajale, 1977), but it is not well differentiated into races.

TAXONOMY OF DOMESTICATED SPECIES

The 2 domesticated species, *E. colona* and *E. crusgalli,* are not always easy to distinguish from one another on herbarium sheets. This is true for both wild and cultivated taxa. In general, *E. crusgalli* is a temperate grass with awned spikelets, while *E. colona* is a more tropical grass with awnless spikelets. But, *E. crusgalli* does extend into the subtropics of Asia and is sometimes characterized by awnless spikelets. The systematics of these 2 species was discussed by Vickery (1975).

1. *Echinochloa crusgalli* (L.) P. Beauv., Ess. Agrost. 53: 161. 1812. Based on *Panicum crusgalli* L., Sp. Pl. 56. 1753. For synonomy see Hitchcock (1950).

Inflorescences are up to 25 cm long with the racemes somewhat spreading. The lower racemes are often shortly branched, with branch and nodal setae commonly numerous. Spikelets are 2.7–4.0 mm long, more or less irregularly arranged on the rachis, and usually awned or at least acute or cuspidate. The upper glume and lower lemma are chartaceous, more or less glabrous between the nerves, usually awned, and with tough spinules along the nerves and along their margins. It is distributed widely in the temperate parts of Eurasia and was introduced to the rest of the temperate world as a weed. Weedy representatives are recognized in the United States as barnyard grass. Populations often segregate into plants with awned spikelets, essentially awnless spikelets, and a mixture of awned and awnless spikelets on the same raceme. Wiegand (1921) and Hitchcock (1950) confuse cultivated *E. crusgalli* with the Indian domesticated complex of *E. colona*.

Cultivated plants are erect, tufted, annual and up to 100 cm tall. Culms are mostly robust, simple or branched from the upper nodes. Leaf sheaths are glabrous, frequently longer than the internodes.

Ligule is absent, and the ligular area is glabrous and smooth. Leaf blades are linear, tapering to a point, 15–40 cm long, 5–25 mm wide, and essentially glabrous. Inflorescences are erect or slightly nodding, at length exserted from the upper leaf sheath, with the spike-like racemes more or less erect and sometimes incurved at the tip. The primary axis is densely furnished with white setae at the nodes. Racemes are 10–25 in number, purple, more or less sessile, 1–5 cm long and densely multispiculate throughout. The rachis is compressed and angular, with the pedicels short and mostly 2-nate, usually with some setae between the spikelets. Spikelets are persistent at maturity, very crowded, 3–4 mm long, shortly cuspidate but rarely awned. The glumes and lower lemma are chartaceous. The lower glume is about one-third as long as the spikelet. The upper glume is usually shorter than the spikelet, cuspidate, hispid along the nerves, with the nerves and margins sometimes subspinulose. The lower lemma is similar in size and shape to the upper glume. The lower floret is neuter and the upper floret is bisexual. The grain is 2–3 mm long and almost as wide.

Cultivated taxa have $2n = 54$ chromosomes, and hybrids with spontaneous *E. crusgalli* are fully fertile (Yabuno, 1966). *Echinochloa crusgalli* was probably domesticated in Japan and was later introduced to Korea, China and adjacent Russia as a cultivated cereal. Watanabe (1970) presents evidence to indicate that it was grown, or at least used as a cereal in Japan since the Yayoi period dating back at least 4,000 yr.

Selected herbarium specimens of cultivated plants: Japan: Yokohama, *Maximowicz,* collected 1862, K; *Duramann and Co.,* 9 August 1893, K. *China:* Yun-Nan, Yun-Nan-Sen, *Maire 2930,* 28 October 1921, K; Chantong, northern China, *Licent 6354,* 11 August 1921, K; Chekiang, *Hickin,* November 1896, K; Sching-Kiang, northern China, *Hort. Kew 3328,* 8 August 1862, K. *Manchuria:* Lac Honka, *Bohnhof 263,* 21 January 1900, K; River Rureja, Amurensij Province, *Komarov 256,* collected 1895, K.

2. *Echinochloa colona* (L.) Link, Hort. Berol. 2: 209. 1833. Based on *Panicum colonum* L., Syst. Nat. ed. 10, 2: 870. 1759. For synonomy see Hitchcock (1950) and Clayton (1972).

Inflorescences are up to 20 cm long, usually somewhat narrow, with the racemes mostly appressed to the primary axis. The lower racemes are rarely branched, with branch and nodal setae usually few in number. Spikelets are 2.5–3.5 mm long, usually arranged in 4 irregular rows, often actue but never awned. Upper glume and lower lemma are membranaceous, often shortly pubescent between the nerves, and with soft spinules along the nerves and along the margins. The species is characterized by $2n = 54$ chromosomes. It is widely distributed in the tropical and subtropical parts of Africa, Asia and Australia, and was introduced to the New World as a weed. The species is exceedingly variable in inflorescence morphology. The racemes are usually appressed to the primary axis, but the lower racemes are sometimes spreading, as is typical also of some cultivars of the species. Specimens with branched lower racemes often have cuspidate spikelets, resembling awnless specimens of *E. crusgalli.* Such collections from tropical Africa, however, form sterile hybrids with the more typically temperate *E. crusgalli.*

Cultivated plants are erect or geniculate ascending, often tufted, annual and up to 242 cm tall. Culms are slender to robust. Slender plants are decumbent with the culms strongly branched and rooting from the lower nodes. Stout plants are erect, with a few culm branches from the upper nodes. Leaf sheaths are glabrous and usually longer than the internodes. Ligule is absent, with the ligular area minutely pubescent. Leaf blades are linear, gradually tapering to a fine point, 8–38 cm long and 6–40 mm wide, glabrous or with a few long hairs at the base. Inflorescences are variable, decumbent plants are characterized by short racemes that are appressed to the primary axis, while more robust plants have larger, pyramidal shaped inflorescences with spreading lower racemes. Inflorescences are usually erect, rarely drooping. Racemes are few to numerous, densely crowded, with the spikelets arranged in 4 irregular rows on the triquetrous rachis, with a few long setae between the spikelets. Pedicels are 2–4-nate, rarely exceeding 2 mm in length. Spikelets are persistent at maturity, 2–4 mm long, acute but never awned. The glumes and lower lemma are typically membranaceous. The lower glume is about one-third as long as the spikelet and the upper glume somewhat shorter than the spikelet, acute, ciliolate along the margins and minutely pubescent between the nerves. The lower lemma is similar to the upper glume in size and shape. The lower floret is neuter and the upper floret is bisexual. The grain is 2–3 mm long and 1–2 mm wide.

Hybrids between cultivated *E. crusgalli* and cultivated *E. colona* are sterile (Yabuno, 1966). *Echinochloa colona* was domesticated in India. It remains an important cereal only in the tropics and subtropics of India.

Selected herbarium specimens of cultivated plants: India: Tamil Nadu, Madura district, *Herb.*

TABLE 1. PARAMETERS FOR MORPHOMETRIC CHARACTERS OF CULTIVATED RACES IN *Echinochloa colona*.[a]

Days to 50% flowering			
robusta	59.8	(6.1)	45–72
intermedia	46.0	(2.9)	41–54
stolonifera	46.4	(2.1)	42–49
laxa	63.3	(5.4)	55–70
Plant height, cm			
robusta	128.0	(21.4)	65–242
intermedia	81.4	(14.3)	51–120
stolonifera	70.3	(10.3)	53–90
laxa	110.8	(7.3)	100–122
Culm diameter, mm			
robusta	7.7	(1.5)	4–15
intermedia	4.8	(1.3)	3–9
stolonifera	3.5	(0.8)	3–5
laxa	7.8	(1.2)	6–9
No. basal tillers			
robusta	6.0	(2.3)	2–14
intermedia	10.5	(4.4)	4–26
stolonifera	21.1	(3.7)	12–28
laxa	6.7	(1.8)	4–9
Flag leaf length, mm			
robusta	253.5	(43.9)	140–380
intermedia	177.1	(35.8)	100–300
stolonifera	150.0	(45.2)	80–260
laxa	241.7	(51.9)	180–300
Flag leaf width, mm			
robusta	26.3	(5.3)	15–40
intermedia	17.3	(4.9)	6–30
stolonifera	13.5	(4.3)	8–20
laxa	22.2	(6.7)	15–30
Sheath length, mm			
robusta	95.8	(15.5)	50–130
intermedia	75.5	(10.1)	50–100
stolonifera	61.4	(7.7)	50–70
laxa	103.3	(15.1)	80–120
Peduncle length, mm			
robusta	133.4	(34.7)	60–240
intermedia	157.7	(33.6)	95–240
stolonifera	153.6	(25.9)	100–190
laxa	123.3	(15.1)	110–150
Panicle length, mm			
robusta	205.2	(32.5)	130–280
intermedia	132.6	(22.5)	70–200
stolonifera	113.9	(16.0)	100–140
laxa	218.3	(28.6)	180–250
Panicle width, mm			
robusta	37.4	(10.5)	20–80
intermedia	27.8	(7.8)	10–55
stolonifera	23.1	(5.5)	14–30
laxa	32.5	(7.6)	20–40
No. primary branches			
robusta	47.4	(9.0)	24–70
intermedia	22.8	(6.0)	11–45
stolonifera	15.5	(4.3)	9–25
laxa	39.3	(3.2)	36–43
Branch length, mm			
robusta	30.7	(9.6)	20–110
intermedia	28.3	(6.7)	15–50
stolonifera	21.8	(7.0)	15–35
laxa	69.2	(23.3)	40–110
No. spikelet rows			
robusta	5.3	(0.8)	3–8
intermedia	4.8	(0.8)	3–6
stolonifera	3.9	(0.5)	3–5
laxa	4.0	(1.1)	3–5

[a] Mean, standard deviation and range are indicated for each character; n = 147 for race robusta, n = 77 for race intermedia, n = 14 for race stolonifera and n = 6 for race laxa.

Bourne, 28 November 1898, K, races robusta and stolonifera; Tamil Nadu, Bellary, Alur Jaluq, *Burkill 21421,* K, race robusta; Tamil Nadu, Rampa district, Rampa Hills, *Naryanaswami 112,* K, race intermedia; Bihar and Orissa, Chaibana, *Haines 5288,* K, race intermedia; Orissa, Daspalla, *Mooney 1794,* K, race stolonifera; Maharashtra, Waghai, Daugs, *Santapau 19242,* K, race intermedia; Kalahandi State, *Mooney 1762,* K, race stolonifera; Kalahandi State, *Mooney 1761,* K, race robusta; Bengal, Nonghyr, *Nokim 1406,* October 1894, K, race stolonifera; Rozi fort near Jamnagar, Nawanagar, *P.v.B.,* 16 October 1945, K, race stolonifera; Northwestern Himalaya, Chamba, *Gammie 18532,* 5 September 1896, K, race robusta; Kashmir, Simla, *Gamble 4906A,* 26 August 1877, K, race robusta. *Sikkim,* Kulimkung, *Gamble 10527,* July 1882, K, race robusta; Chakoong, *Hooker,* collected October–November 1849, K, this collection includes races robusta, intermedia, stolonifera and laxa on the same herbarium sheet.

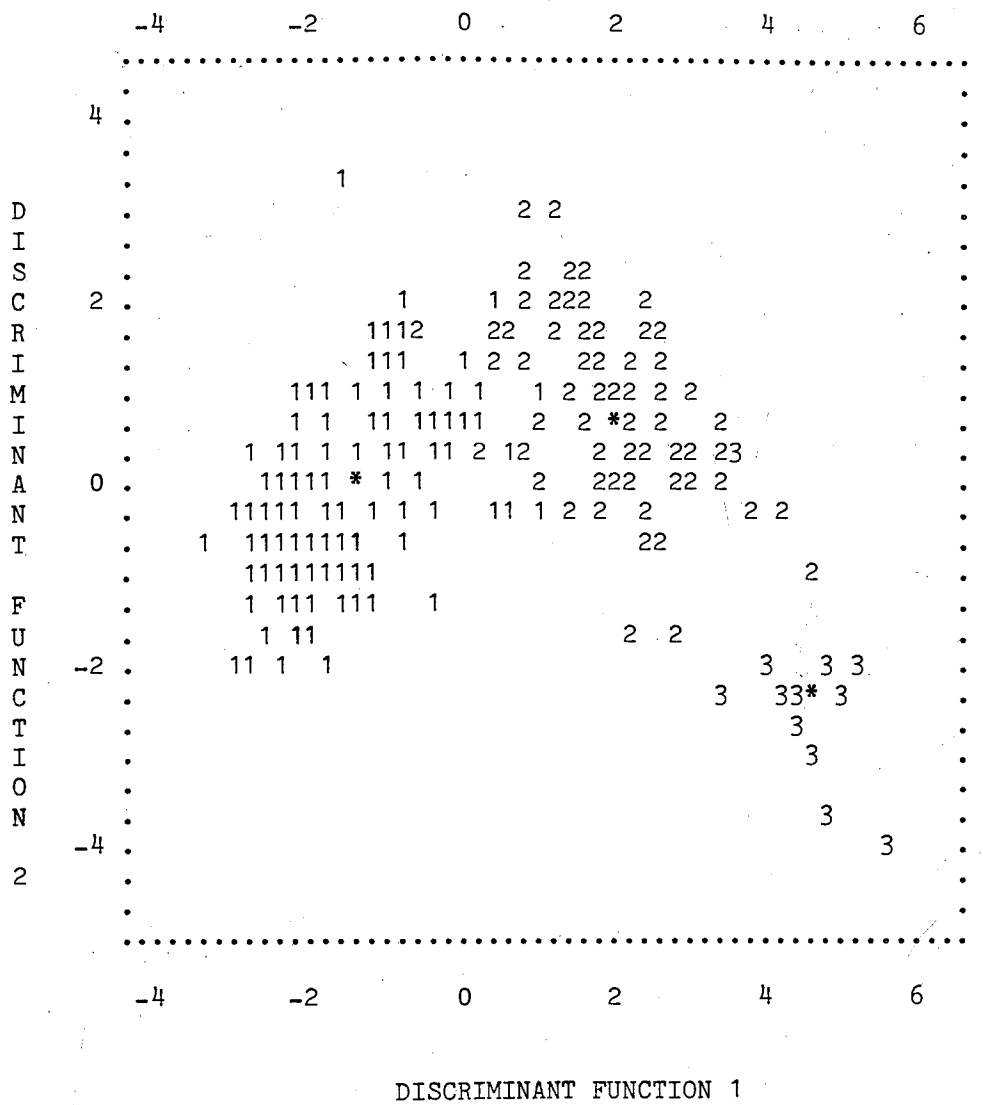

Fig. 1. Plot of OTUs on the 2 discriminant functions. 1 = race robusta, 2 = race intermedia, 3 = race stolonifera. Group centroids (average discriminant function scores) are indicated by asterisks for races 1–3. OTUs falling on a previously occupied space were deleted. Consequently, not all OTUs are plotted, and OTUs are somewhat more tightly grouped around their respective centroids than indicated in this figure.

RACIAL DIFFERENTIATION IN CULTIVATED *E. COLONA*

Collections of *Echinochloa colona* at the International Crops Research Institute for the Semiarid Tropics (ICRISAT) assembled from across India, and consisting of 243 seed samples was grown in a uniform nursery at Patancheru near Hyderabad, and studied in morphological detail for 13 qualitative and 13 quantitative characters. This crop also was studied in farmers' fields in southern Andhra Pradesh. *Sawa* is the common Telugu name for this cereal. It is also known as

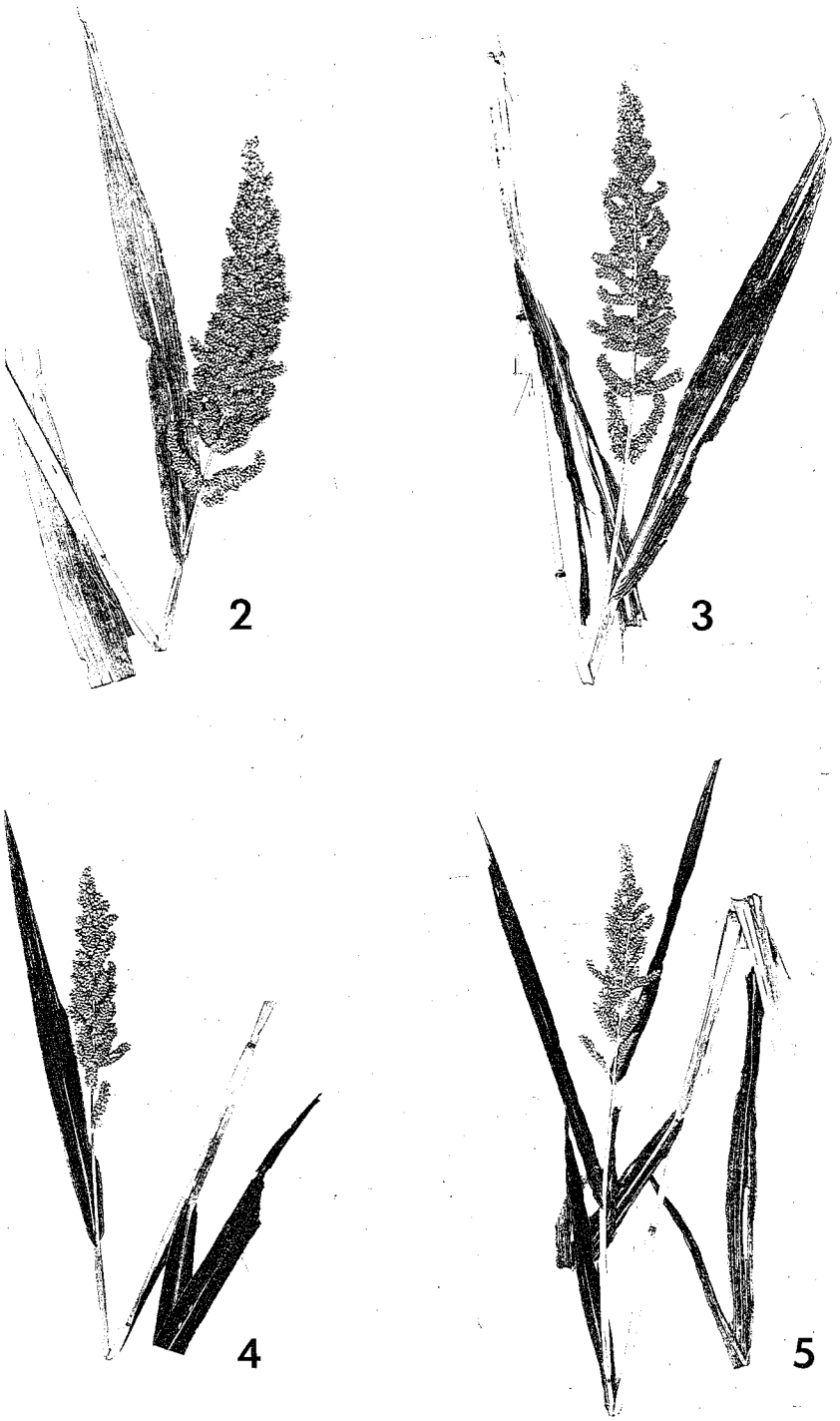

Fig. 2–5. Inflorescence morphology of cultivated *E. colona*. Fig. 2–3. Race robusta (*de Wet 4656*, Oct. 22, 1981, CEL). Fig. 4–5. Race intermedia (*de Wet 4656*, Oct. 24, 1981, CEL).

Fig. 6–9. Fig. 6–7. Race stolonifera (*de Wet 4637,* Oct. 6, 1981, CEL). Fig. 8–9. Race laxa (*de Wet 4639,* Oct. 7, 1981, CEL).

shama in Bengali, *samu* in Urdu, *shamula* and *sanwa* in Hindi, and as *sawu* in Tamil. There are probably many other local names used across the range of its cultivation from southern India to Kashmir and Sikkim.

Farmers commonly grow a variety of morphological types in the same field. An analysis of the data (Table 1), however, suggests 4 morphologically distinct complexes. Interracial differences in 13 quantitative characters cannot be comprehended simultaneously, and discriminant analysis (direct method, Nie et al., 1975) was used to characterize these complexes. This fulfilled several objectives. Discriminant analysis served as a data reduction technique allowing visualization of the extent of racial coherence and overlap in the reduced 2-dimensional space defined by the discriminant functions. Three races were clearly separated and well defined by this analysis with a minimum of overlap among them (Fig. 1). There was a high (93%) correspondence between our initial classification of the plants based upon their overall appearance in the field and the results of the discriminant function classification routine. The fourth race was defined on the basis of qualitative characters.

1. *Race robusta* (Fig. 2–3) is characterized by erect plants up to 242 cm tall, usually with 2–14 culms that branch from the upper nodes. The flag leaf is up to 38 cm long and 40 mm wide, with the inflorescence exserted from the 5–13 cm long sheath. The peduncle is 6–24 cm long, and supports a 13–28 cm long inflorescence composed of 24–70 racemes. Racemes are up to 110 mm long, with the lower racemes spreading out from the primary axis at an angle of 45–85°, with their tips curved inward, and the upper ones more or less appressed to the primary axis, giving the inflorescence a pyramidal appearance.

2. *Race intermedia* (Fig. 4–5) is intermediate in morphology between races robusta and stolonifera and it often intergrades with these larger and smaller races. Plants are more or less erect, up to 120 cm tall, usually with 4–26 culms that frequently branch and often root from the lower nodes. The flag leaf is 10–30 cm long and 6–30 mm wide, with the inflorescence exserted from the 5–10 cm long sheath. The peduncle is 10–24 cm long and supports a 7–20 cm long inflorescence that is composed of 11–45 racemes. Racemes are 15–50 mm long and spread out from the primary axis at an angle of 15–25°, with the tips curved inward, often touching the primary axis.

3. *Race stolonifera* (Fig. 6–7) is characterized by decumbent plants up to 90 cm tall, with as many as 28 culms that branch profusely and root at the lower nodes. The flag leaf is 8–26 cm long and 8–20 mm wide, with the inflorescence well exserted from the 5–7 cm long sheath. The peduncle is 10–19 cm long, and supports a 10–14 cm long inflorescence composed of 9–25 racemes. Racemes are up to 35 mm long, more or less appressed to the primary axis with the tips often curved inward.

4. *Race laxa* (Fig. 8–9) is known only from a few Sikkim collections. It is characterized by long, slender racemes that are strongly branched and pendent or appressed to the primary axis. Plants are robust and erect, up to 122 cm tall, with 4–9 culms that rarely branch. The flag leaf is up to 30 cm long and 30 mm wide, with the inflorescence exserted from the 8–12 cm long sheath. The peduncle is 11–15 cm long and supports an 18–25 cm long panicle that is composed of 36–43 primary branches. Racemes are 40–110 mm long, slender, strongly branched and pendent.

The strongly branched racemes of race laxa suggest affinities with *E. crusgalli*. Race laxa however, resembles *E. colona* in spikelet morphology. Furthermore, herbarium studies indicate that all 4 cultivated races of *E. colona* are grown in Sikkim, while cultivated *E. crusgalli* has never been collected on the Indian subcontinent. Race laxa is similar in most characters to race robusta (Table 1), and in classification using the discriminant functions computed for the 3 major races, laxa collections all plotted among accessions of race robusta. Race laxa, however, is distinguished by its slender, lax racemes which distinguish it from race robusta (Fig. 8–9).

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