A Revision of the Infraspecific Taxonomy of *Cyperus esculentus* (Yellow Nutsedge) with an Experimentally Evaluated Character Set

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ABSTRACT. *Cyperus esculentus* (Yellow Nutsedge) is a troublesome weed with broad infraspecific variation. A growing experiment was performed in which diverse clones were raised under different environmental conditions. Sixty five characters were measured and evaluated based upon their sensitivity to environmental and clonal differences. Of these, 17 proved to be sufficiently reliable for taxonomic purposes. They concern size and shape of floral parts rather than dimensions of spikes, which were until now thought to be the diagnostic characters. Herbarium material from all continents where *C. esculentus* is present was studied, including type material of varieties; 70 plants were selected, the 17 parameters measured, and the data analysed by multivariate techniques. Four clusters were distinguished, which appeared to broadly represent four varieties described by Kükenthal in 1935; three of his seven varieties were rejected, var. *cyclolepis*, var. *nervoso-striatus*, and var. *sprucei*. The four remaining varieties are discussed and described, and a key is given for their identification. They are var. *esculentus*, var. *leptostachyus*, var. *macrostachyus*, and var. *heermannii*. All of these varieties occur in the Americas as well as in Europe. Variety *esculentus* dominates in Africa and southern Europe, var. *leptostachyus* is rather common in both the Old and the New World. Two varieties, var. *macrostachyus* and var. *heermannii*, have been recently introduced into the Netherlands; they probably originate from the Americas. The occurrence of var. *leptostachyus* in Europe is probably the result of an earlier introduction.

Cyperus esculentus L., Yellow Nutsedge, is a troublesome perennial weed with a worldwide distribution. It is present on all continents except Antarctica and it is a serious pest in at least 10 countries (Bendixen and Nandihalli 1987). Holm et al. (1977) regarded it as the world's 16th worst weed. Its range has recently expanded through migrations into N.W. Europe (Rotteveel 1993; Ter Borg and Schippers 1992; Van Groenendael and Habekotté 1988). Although Yellow Nutsedge produces viable seeds, the weed usually spreads by means of the small tubers produced on the rhizomes, and hence a population in a single field may be the progeny of one or only a few genotypes (Horak and Holt 1986).

Although Horak and Holt (1986) found little variation within populations of this clonal species, morphological variation between populations appeared to be fairly wide. *Cyperus esculentus* was reported to be variable in respect to a number of agriculturally important characters: e.g., response to herbicides (Costa and Appleby 1976; Hauser 1968; Schippers et al. 1993); tuber size, day length requirements, and aggressiveness related to length and depth of rhizomes (Yip 1978 a, b); susceptibility to winter kill (Matthiesen and Stoller 1978); frost tolerance of tubers and effects of shading (Ter Borg et al. 1988). According to Cavers (1985), the problem of intraspecific variation in weed species will become increasingly important in the near future because of plant introduction and selection by new methods of weed control.

The first study of the infraspecific taxonomy of Yellow Nutsedge was done by Boeckeler

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(1870) who reduced two American species, *C. phymatodes* H.L. Mühl. and *C. lutescens* Torr. & Hook. to *C. esculentus* var. *leptostachyus* Boeckeler and var. *macrostachyus* Boeckeler, respectively. Moreover, he recognized a cultivated taxon, *C. esculentus* var. *sativus* Boeck. (known as earth almond, tiger nuts, or chufa) which is distinguished by its large edible tubers.

In 1884, Clarke described *C. esculentus* var. *sprucei* Clarke, and Britton (1886) distinguished var. *angustispicatus* Britton. The latter author also reduced *C. heermannii* Buckley to *C. esculentus* var. *heermannii* (Buckley) Britton. Ascherson and Graebner (1902–1904) divided the species in two races: the edible, cultivated *sativus*, and *aureus*, including all wild and weedy material. De Vries (1991) proposed cv. *Chufa* for the cultivated taxon.

In an extensive revision of Cyperaceae, Kükenthal (1935) reviewed the varieties mentioned and described two more, var. *nervoso-striatus* (Turrill) Kük. (= *C. nervoso-striatus* Turrill) and var. *cyclolepis* Boeck. ex Kük. Table 1 summarizes the morphological characteristics of the seven weedy varieties he distinguished based on characters of the inflorescence only. Kükenthal's study included herbarium material from North and South America, Africa, southern Europe, the Middle East, and India. Based on Kükenthal's work, var. *esculentus* has the widest range, with most of the accessions (85) originating from Africa, 16 recorded from North and South America, 22 from southern Europe, two from the Middle East, and nine from India. Two varieties, var. *nervoso-striatus* and var. *cyclolepis* were restricted to southern and eastern Africa, and were represented by one and two sheets, respectively. The three other varieties originated from the Americas, with var. *leptostachyus* the most common (67 citations). Variety *macrostachyus*, var. *sprucei*, and var. *heermannii* were cited 12, six and four times, respectively.

Certain American floras reduced the rank of the taxa, and distinguished a number of forms within var. *esculentus* [f. *esculentus*, f. *angustispicatus* (Britt.) Fern. and f. *macrostachyus* (Boeckl.) Fern.], with differences mainly based on size of the spikelets (Fernald 1950; Steyermark 1963). Mohlenbrock (1960) maintained the level of variety, included additional characteristics when describing them, and changed their circumscriptions without discussion.

Stoller and Sweet (1987), reviewing the American literature on physiological and ecological variation within *C. esculentus*, pointed to problems in classification and indicated several inconsistencies. In a preliminary report on the infraspecific variation of *C. esculentus* in the Netherlands Ter Borg et al. (1988) described four biotypes (A-D), including data on vegetative characters. They had difficulties establishing the taxonomic position of their material.

Since the difficulties of Ter Borg et al. (1988) could be due to plasticity of the characters commonly used for identification, an experimental study was undertaken to evaluate the taxonomic value of a range of morphological characters of *C. esculentus*. Characters with low sensitivity to environmental variation were considered taxonomically important and were selected for a multivariate numerical analysis. The results formed the basis for an evaluation of the taxa described by Kükenthal (1935), a revision of the infraspecific taxonomy of *C. esculentus*, and an assessment of the geographic distribution of the infraspecific taxa.

MATERIALS AND METHODS

Testing Character Reliability. Clones of *C. esculentus*, raised from single tubers collected in six populations were kept in an experimental garden since 1987. These clones covered the variation observed in the Netherlands and included the four biotypes, A-D, distinguished by Ter Borg et al. (1988). Biotypes A and B were represented by two populations and biotypes C and D by one each. Voucher specimens collected in the garden are deposited in Herbarium Vadense (WAG) under the following numbers:

A-EK, arable land, S.E. Netherlands, Elsendorp: *De Nijs 6001*.

A-BT, arable land, S.W. Netherlands, Bath: *De Nijs 6301*.

B-EW, arable land, S.E. Netherlands, Elsendorp: *De Nijs 6701*.

B-MB, arable land, N.W. Netherlands, Maartensbrug: *De Nijs 4801*.

C-MK, arable land, C. Netherlands, Markelo: *De Nijs 7401*.

D-SB, arable land, S.E. Netherlands, Sambeek: *De Nijs 7101*.

In March 1990, tubers were taken from one clone each of these six populations and plants

TABLE 1. *Cyperus esculentus* varieties according to Kükenthal (1935), "=" indicates that this character does not deviate from the state in var. *esculentus*.

Character	Esculentus	Cyclolepis	Nervoso-striatus	Macrostachyus	Sprucei	Leptostachyus	Heermannii
Flower							
achene	normal	=	broad	=	=	=	=
stigmata	normal	=	=	=	long	=	=
Floral scale							
form	variable	obovoid	=	obtuse	=	obtuse	obtuse
tip	variable	truncate	=	mucronate	=	mucronate	mucronate
color	green-yellow or red-dish at the edge	=	=	brown	yellow-brown	red-brown	red-brown
Spikelet							
length (mm)	5–12	<5	=	≤30	≤30	15–20	15–20
width (mm)	2.0	=	=	≤3.0	3.0–4.0	1.5	1.5
flowers/spikelet	8–16	4–6	=	≤40	≤48	=	=
imbrication	normal	=	=	close	loose	loose	loose
form	normal	oval	=	=	=	=	=
Spike							
spikelets/spike	5–14	=	=	many	=	many	=
spikelet angle	normal	=	=	=	=	=	small
spikelet density	low	=	high	=	=	=	very high
involucral secondary bracts	no	=	=	=	=	=	yes
Culm, Bracts, and Inflorescence							
inflorescence	simple-complex	=	=	=	=	complex	complex
culm compressed	yes	=	=	no	=	=	=
number of primary bracts	3–6	=	=	=	=	=	9–13
number of rays	5–10	=	=	=	=	=	11–13

TABLE 2. *Cyperus esculentus* L. morphological characters scored; also see Fig. 1.

Designation	Character description
Flower	
F1	Length of the stylar branch.
F2	Length of the undivided part of the style.
F3	Length of ovary.
F4	Width of ovary.
F5	Distance from the base of the ovary to the place where the ovary has its maximum width.
F6	Length of the anthers in fully developed flower.
F7	Length of the filament in fully developed flower.
F8	Ratio between stylar branch and glume length (F1/G10).
F9	Ratio between filament and glume length (F7/G10).
F10	Width/length ratio of the ovary (F4/F3).
F11	Ratio between stylar branch and style (F1/F2).
Floral scale	
G1	Length of a floral scale near the top of a spikelet.
G2	Length of a floral scale in the middle of a spikelet.
G3	Length of a floral scale near the base of a spikelet.
G4	Maximum width of a floral scale in the middle of a spikelet measured from the side of the floral scale to the midnerve $\times$ 2.
G5	Distance from the base of a floral scale to the place where it has its maximum width.
G6	Ratio between floral scale length at the base of the spikelet and mean floral scale length (G3/G10).
G7	Width/length ratio of the floral scale (G4/G2).
G8	Ratio between height where the floral scale reaches its maximum width and length of a floral scale (G5/G2).
G9	Ratio between length of a floral scale at the top of the spikelet and the mean length of the floral scales (G1/G10).
G10	Mean floral scale length [(G1 + G2 + G3)/3].

TABLE 2. Continued.

Designation	Character description
Spikelet	
S1	Number of scales of spikelet number 1 (spikelet selected at random).
S2	Number of scales of spikelet number 2 (spikelet selected at random).
S3	Number of scales of spikelet number 3 (spikelet selected at random).
S4	Length of spikelet number 3.
S5	Width of spikelet number 3 at 1 mm from the top.
S6	Width of spikelet number 3 measured in the middle.
S7	Width of spikelet number 3 at the base.
S8	Thickness of a spikelet.
S9	Length of a prophyll of a spikelet.
S10	Length of a bract of a spikelet.
S11	Ratio between spikelet prophyll and bract (S9/S10).
S12	Ratio between scale angle (top of spikelet) and mean scale angle (S15/S19).
S13	Ratio between scale angle (middle of spikelet) and mean scale angle (S16/S19).
S14	Ratio between scale angle (base of spikelet) and mean scale angle (S17/S19).
S15	Floral scale angle near the top of a spikelet ($\times$ = multiplication). [(360/2π) $\times$ ARCSIN (0.5 $\times$ S5/G1)].
S16	Floral scale angle at the middle of a spikelet [(360/2π) $\times$ ARCSIN (0.5 $\times$ S6/G2)].
S17	Floral scale angle near the base of a spikelet [(360/2π $\times$ ARCSIN (0.5 $\times$ S7/G3)].
S18	Mean number of scales per spikelet [(S1 + S2 + S3)/3].
S19	Mean scale angle [(S15 + S16 + S17)/3].
S20	Density of floral scales on a spikelet [S3/(S4-G2)].
Spike	
E1	Number of primary rays per plant, including the smallest visible.

TABLE 2.   Continued.

Designation	Character description
E2	Maximum length of a primary ray from the base to the top of the spikelet.
E3	The second maximum length of the primary rays.
E4	Maximum number of spikelets per spike.
E5	Maximum number of spikelets of the second order rays per spike.
E6	Number of second order rays per spike.
E7	Maximum length of the rachis.
E8	Angle between spikelets and rachis.
E9	Spikelet density on a spike [(E4 + E5)/E7].
E10	Ratio between number of rays and culm thickness (E1/C7).
Culm and bracts	
C1	Length of the culm.
C2	Maximum length of the bracts.
C3	Second maximum length of the bracts.
C4	Third maximum length of the bracts.
C5	Width of the largest bract at 5 cm from the base.
C6	Thickness of the largest bract at 5 cm from the base.
C7	Maximum thickness of the culm 5 cm under the inflorescence.
C8	Number of bracts, including the smallest visible.
C9	Ratio between culm length and width (C1/C7).
C10	Ratio between bract width and culm width (C5/C7).
C11	Number of rays/number of bracts (both including the smallest visible) (E1/C8).
Leaves	
L1	Length of the longest leaf.
L2	Length of the second-longest leaf.
L3	Length of the third-longest leaf.

were grown in greenhouses in 3-liter pots with a soil mixture of 75% sand and 25% potting compost. Growth conditions for these greenhouse plants from April 27 to August 7 in Wageningen

were varied as follows: soil fertility (0.318 g N/pot and no N application), temperature (22°C and 18°C constant temperature) and daylength (natural long days, natural daylengths for one month changed to 12-hour cycles of light and dark for the remainder of the season, and 12-hour cycles of light and dark during the entire growing season). An additional set of plants from each of the six populations was grown in outdoor experimental plots under natural conditions in Wageningen during the season of 1987. These natural outdoor conditions were considered a separate treatment, yielding eight treatments in total.

Plants were harvested and dried after flowering. From each treatment and each clone, at least one flowering primary shoot, if available, was chosen along with the smallest (flowering) secondary shoot. Shoot status (i.e., primary or secondary shoot) was considered a further variable to be tested. Forty characters were measured, including those used by Kükenthal (1935), as indicated in Table 2. However, form and color of spikelets were difficult to assess quantitatively and were not studied. Another 24 characters were calculated and derived from the 40 primary values, yielding a total of 65 variables. These almost exclusively concern characters of the inflorescence (Fig. 1; Table 2).

Analysis of variance was performed for unbalanced design to test character dependence on genetic background, environmental conditions, and shoot status. Data were analysed using the GLM procedure of the SAS 6.0 statistical package (SAS Institute Inc. 1985).

Clustering and Ordination.   Herbarium material was studied from two main sources.

1) About 1,000 C. esculentus vouchers from various herbaria (B, BM, K, L, MO, PRE, US, WAG) were examined. After an initial review, 50 of them, from 41 populations covering the range of variation on a global scale and usually cited by Kükenthal (1935), were selected for numerical analysis. This group included the range of variation described by Kükenthal, and the type material of five varieties: var. heermannii, var. sprucei, var. cyclolepis, var. macrostachyus, and var. nervoso-striatus.

2) In the Netherlands 136 inflorescences were collected from the field or from plants grown in pots in the greenhouse or the experimental garden. They were dried and deposited in Herbarium Vadense (WAG). Of these, 20 that cov-

TABLE 3. *Cyperus esculentus* plants measured. Identifications according to Kükenthal (1935). ES = var. *esculentus*, LE = var. *leptostachyus*, MA = var. *macrostachyus*, HE = var. *heermannii*, NE = var. *nervoso-striatus*, CY = var. *cyclolepis* and SP = var. *sprucei*. A, B, C, and D are biotypes described by Ter Borg et al. (1988), (1) = determined by Kükenthal but not mentioned in Kükenthal (1935); (2) = determined by other authors; (3) = type material.

Popu-lation number	Origin Continent, Country	Origin Place	Number of plants	Identifi-cation	Collector numbers and herbarium
1	Eu. Netherlands	Elsendorp K	3	A	*De Nijs 6010, 6045, 6052* (WAG)
2	Eu. Netherlands	Elsendorp L	4	B	*De Nijs 6908–6911* (WAG)
3	Eu. Netherlands	Elsendorp S	1	D	*De Nijs 5808* (WAG)
4	Eu. Netherlands	Elsendorp A	3	C/B	*De Nijs 7005, 7018, 7020* (WAG)
5	Eu. Netherlands	Oosterland	1	A	*De Nijs 6114* (WAG)
6	Eu. Netherlands	Maartensbrug	1	B	*De Nijs 3540* (WAG)
7	Eu. Netherlands	Boxmeer	3	D	*De Nijs 7101, 7104, 7109* (WAG)
8	Eu. Netherlands	Markelo	4	C/D	*De Nijs 7407, 7415, 7417, 7418* (WAG)
50	Eu. Turkey	Pontus	1	ES	*Sintenis 1417* (K)
51	Eu. France	Mentone	2	ES	*Moggridge s.n.* (US)
52	Eu. France	Corsica	1	ES	*Mabile 285* (K)
53	Eu. Spain	Segorbe	1	ES	*Reverchon s.n.* (US)
54	Eu. Italy	Napoli	2	ES	*Tenore s.n.* (K)
55	Eu. Italy	Palermo	1	ES	*Todaro s.n.* (K)
56	Af. Zimbabwe	Cheshire	1	ES	*Exped. Suecica in Africam, Austr. et Rhodesiam 4424* (BM)
57	Af. Ethiopia	Tigre	1	ES	*Schimper 1246* (BM)
58	Af. Egypt	Damiette	1	ES	*Sieber 393* (K)
59	Af. Tanzania	Malongwe	1	ES	*Peter 34633* (K)
60	Af. Sierra Leone	Niger (river)	1	ES	*Vogel 31* (K)
61	Af. Senegal	?	1	ES	*Trochain 171* (K)
62	Af. Central Afr.	Bambari	1	ES	*Tisserant 1503* (K)
63	Af. Tanzania	Kilimandscharo	1	ES	*Volkens 2111* (K)
64	Af. Tanzania	Ruhudje (river)	1	ES	*Schlieben 1931* (K)
65	Af. Mozambique	Zambesia	1	ES	*Buchanan 23* (K)
66	Af. South Afr.	Pretoria	3	CY(3)	*Rehmann 4776* (B, K)
67	Af. South Afr.	Ermelo	1	NE(3)	*Burtt-Davy 9237* (PRET)
68	NA. California	?	2	HE(3)	*Heermann s.n.* (US)
69	NA. Utah	Moab	1	HE(2)	*Parrish s.n.* (US)
70	NA. Texas	?	3	MA(3)	*Drummond 452* (B, BM, K)
71	NA. Texas	El Paso	1	MA	*Wright 705* (BM)
72	NA. California	San Diego	1	MA	*Orcutt 1314* (US)
73	NA. Florida	Duval Co.	3	LE	*Curtiss 3052* (K, US)
74	NA. Missouri	St. Louis	1	LE	*Drummond 61* (B)
75	NA. Illinois	Bornizet?	1	LE(1)	*Anon. s.n.* (B)
76	NA. Mississippi	New Orleans	1	LE	*Drummond 387* (B)
77	NA. Missouri	St. Louis	1	LE(1)	*Eggert s.n.* (B)
78	NA. California	Sacramento	1	LE	*Jones 3529* (BM)
79	NA. Oklahoma	Tishomingo	1	LE	*Palmer 6454* (US)
80	NA. Texas	Comanche Spring	1	ES	*Lindheimer 1237* (K)
81	CA. Dominican Rep.	Santo Domingo	1	LE	*Ekman 14084* (K)
82	CA. Haiti	Vaillecite	1	LE	*Ekman 6103* (US)
83	CA. Mexico	Morelia	1	LE	*Arsène 5231* (BM)
84	CA. Mexico	Orizaba	1	ES	*Bourgeau 2386* (US)
85	CA. Mexico	Rancho Pasadat	1	ES	*Nicolas s.n.* (US)
86	CA. Mexico	Guadahyze	1	ES	*Bourgeau 526* (US)
87	SA. Paraguay	Rica	1	LE(1)	*Jörgensen 3575* (B)
88	SA. Brazil	Pardo	1	LE(1)	*Jurgens 97* (B)
89	SA. Ecuador	Chanduy	1	SP(3)	*Spruce 6414* (K)
90	AS. India	Madras	1	ES	*Thomson 69* (K)

ered the range of morphologic variation observed in the Netherlands were selected for detailed measurements. They represent eight populations.

The 70 plants selected for this study (Table 3) were screened for the characters chosen according to the results of the experimental evaluation. Data were standardized and preprocessed with the ACECLUS procedure of the SAS statistical package. Canonical variables from this procedure were used for clustering and ordination. Relationships among the plants were analyzed with Wards minimum variance method of the CLUSTER procedure (SAS Institute Inc. 1985).

Results of the clustering analysis were compared with the classification by Kükenthal (1935) and the geographic origin of the selected plants. The characters of contradictory specimens were compared, and individual plants were reclassified as necessary. Based on this analysis, descriptions of four varieties were revised and their geographic distribution indicated.

RESULTS

Character Reliability. Clones did not flower in every situation. Clones A-EK and C-MK flowered under all conditions, except short days, where none of the clones produced an inflorescence. Shoots of clone C-MK did not grow under short day conditions, but did produce a few tubers. Clones B frequently produced flowers under higher temperatures; under other conditions B usually produced a culm with bracts only. Fifty-three flowering shoots were harvested and their data used for statistical analysis.

Table 4 summarizes the results of the analysis of variance. In 44 out of 65 cases, characters differed significantly between clones, and 31 characters were shown to be sensitive to environmental variation or shoot status. Based on these results four groups of characters were distinguished.

Group 1 includes the most important characters, since they differ significantly between clones and are stable with respect to variable growing conditions and shoot status. The characters in group 2 vary between clones also, but they are affected by environmental conditions and shoot status and can be useful only when the effect of clonal background is high com-
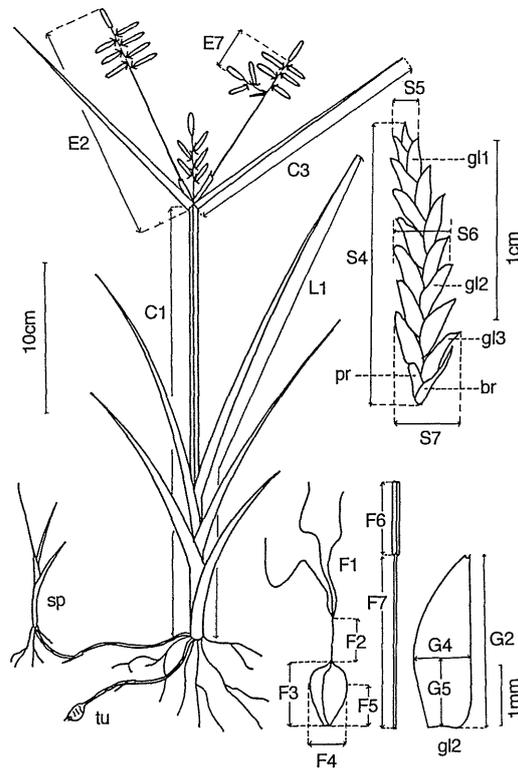

FIG. 1. Schematic drawing of *Cyperus esculentus* showing some characters described in Table 4. gl1, gl2 and gl3 = floral scales (glumes) from which characters G1, G2 and G3 have been measured; pr = prophyll, br = bract of a spikelet from which S10 was measured, sp = secondary shoot, tu = tuber.

pared to other sources of variation. However, under uniform conditions these characters can be as important as characters of group 1.

Group 3 consists of characters that show no significant differences and therefore can not be used in distinguishing the clones included in this experiment. However, they can be excellent characters separating other clones. Characters in group 4 have no taxonomic value. They did not differ among the clones studied; their variation is due to other factors.

Characters were chosen for further taxonomic treatment using the following criteria: 1) high between-clone variation compared to variation caused by environmental differences or shoot status, and 2) low suspected dependence upon other selected characters. Seventeen characters indicated in Table 4 were selected, 13 from group 1, three from group 2, and one from group 3.

TABLE 4. F values in the analysis of variance, testing the effect of clonal origin, environmental conditions, and shoot status on morphological characters of *Cyperus esculentus* (* $P < 0.01$; ** $P < 0.001$; *** $P < 0.0001$). (S) = characters selected for numerical analysis. (K) = characters used by Kükenthal (1935).

| | Source of variation | | | | |
| | Clone
d.f. = 5
F value | Environment
d.f. = 6
F value | Shoot status
d.f. = 1
F value | Characters
selected | Used by
Kükenthal (1935) |
Designation					
Group 1 Characters					
G5	39.22***	0.11	0.20	(S)	—
G4	35.27***	2.73	2.63	(S)	—
F1	33.46***	1.41	0.05	(S)	(K)
C11	23.47***	0.89	3.32	(S)	—
E10	21.80***	1.43	0.02	—	—
S1	20.69***	1.86	6.93	(S)	(K)
S19	20.45***	1.05	4.11	—	—
E6	18.52***	2.22	4.10	(S)	(K)
E9	16.37***	0.79	1.68	(S)	(K)
S2	15.40***	2.54	6.66	—	—
F7	14.09***	1.63	0.40	—	—
E8	12.91***	2.26	4.80	(S)	(K)
S16	10.51***	0.55	0.01	(S)	—
S15	10.03***	0.88	0.60	—	—
S11	8.62***	1.66	0.20	(S)	—
F2	8.05***	0.52	1.47	(S)	—
E5	7.64***	2.01	3.24	—	—
S10	6.29**	2.30	4.63	—	—
F9	5.51**	2.45	1.19	—	—
F11	5.07*	1.30	0.96	—	—
S12	4.32*	0.99	0.01	—	—
G7	4.12*	2.58	0.08	—	—
G9	3.83*	3.01	0.26	(S)	—
F6	3.69*	1.46	2.13	(S)	—
Group 2 Characters					
G10	72.98***	8.47***	2.65	(S)	—
G1	68.14***	10.71***	1.27	—	—
G2	57.63***	6.97***	4.01	—	—
S20	51.66***	10.05***	3.03	(S)	(K)
G3	31.77***	3.97*	0.90	—	—
S3	18.58***	2.06	7.67*	—	—
E1	17.06***	2.45	22.42***	—	—
E7	14.43***	3.66*	30.19***	—	—
S4	13.09***	3.27	9.05*	—	(K)
S18	12.39***	3.01	7.60*	—	(K)
S17	11.35***	1.93	10.76*	—	—
F8	10.24***	5.28**	1.11	—	—
S9	9.48***	3.89*	10.90*	—	—
G8	6.95***	3.42*	3.39	—	—
E4	6.53**	5.61**	30.40***	—	(K)
C2	5.68**	40.57***	63.25***	—	—
C8	4.85*	4.66*	37.91***	—	(K)
L1	4.42*	53.15***	67.76***	—	—
C9	4.18*	20.97***	1.32	—	—
G6	4.12*	3.54*	0.98	(S)	—

TABLE 4.   Continued.

Designation	Clone d.f. = 5 F value	Environment d.f. = 6 F value	Shoot status d.f. = 1 F value	Characters selected	Used by Kükenthal (1935)
Group 3 Characters					
C10	2.70	1.13	6.48	—	—
F4	2.39	1.40	3.09	—	(K)
S5	1.97	1.37	0.70	—	—
F5	1.94	2.75	1.20	—	—
F10	1.87	2.78	2.93	(S)	(K)
C6	1.28	1.64	2.57	—	—
S14	1.21	1.61	5.18	—	—
S8	1.12	2.90	0.06	—	—
F3	0.64	2.03	0.00	—	—
L3	0.55	2.68	2.91	—	—
Group 4 Characters					
S13	3.41	1.43	8.40*	—	—
C1	3.16	15.54***	22.66***	—	—
S6	2.79	5.38**	1.42	—	(K)
L2	2.65	42.37***	58.33***	—	—
C3	2.35	22.42***	51.04***	—	—
C7	2.20	3.59*	48.80***	—	(K)
S7	1.91	3.84*	16.65**	—	—
E3	1.88	4.73**	32.24***	—	—
E2	1.78	5.63**	32.50***	—	—
C4	0.85	12.79***	46.90***	—	—
C5	0.68	2.30	21.65***	—	—

Cluster Analysis. Figure 2 presents the results of the cluster analysis of the 70 plants included in this study (Table 3). Their classification according to Ter Borg et al. (1988) and Kükenthal (1935) are indicated as well as their geographic origins. The analysis shows four main clusters.

Figure 3 gives the ordination diagrams of the same plants, showing their position according to cluster number (Fig. 3A), taxonomic position (Fig. 3B), or geographic origin (Fig. 3C). There are no distinct clusters in Fig. 3. However, there is a clear relationship between cluster borders and classification (Fig. 3B), and geographic origin (Fig. 3C).

In general the position of plants from the American continents (Fig. 2, clusters 1, 3, and 4) is clearly distinct from that of plants from other continents, most of which belong to cluster 2. Only 4 plants did not fit into this pattern (outlined in Fig. 3), viz. Reverchon s.n. (US); Trochain 171 (K); Volkens 2111 (K); Thomson 69 (K); (Table 3, numbers 53, 61, 63 and 90). These four plants were classified as var. esculentus by Kükenthal and appear to be on the edge of cluster 2 according to the ordination. Therefore it seems to be justified to consider these plants var. esculentus.

All clusters but number 1 were found to be rather homogeneous, and dominated by a single variety; cluster 2 is dominated by var. esculentus, cluster 3 by var. heermannii, and cluster 4 by var. leptostachyus.

Apart for the single exception of De Nijs 7005 (WAG), (Table 3, no. 4), all plants belonging to the four biotypes distinguished in the Dutch material were found grouped, each group in a separate cluster (Fig. 2).

Cluster 1 appears to include four varieties, none of which predominates. Six plants had been identified as var. esculentus by Kükenthal, five as var. macrostachyus, four as var. leptostachyus, and one as var. sprucei. Most of these originate from the Americas and only two from Africa; the latter already have been assigned as var. esculentus. Table 5 gives the data on floral
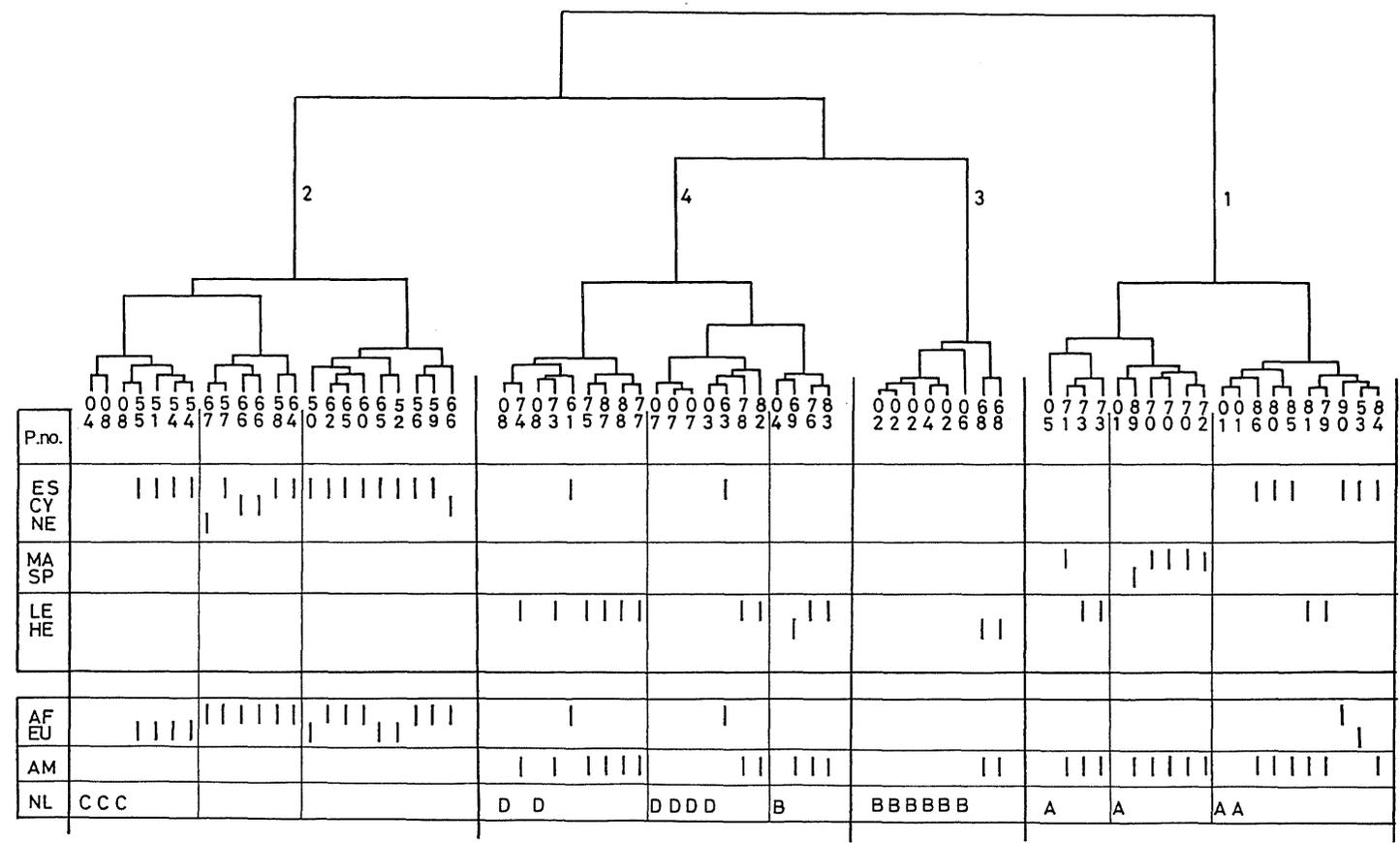
2　　4　　3　　1

P.no.	0 0 0 5 5 5 5	6 5 6 6 5 6	5 6 6 6 6 5 5 5 6	0 7 0 7 6 7 8 8 7	0 0 0 0 6 7 8	0 6 7 8	0 0 0 0 0 0 6 6	0 7 7 7	0 8 7 7 7 7	0 0 8 8 8 8 7 9 5 8
	4 8 8 5 1 4 4	7 7 6 6 8 4	0 2 5 0 5 2 6 9 6	8 4 8 3 1 5 7 8 7	7 7 3 3 8 2	4 9 6 3	2 2 2 4 2 6 8 8	5 1 3 3	1 9 0 0 0 2	1 1 6 0 5 1 9 0 3 4
ES CY NE	I I I I I I I I I I I I I I I I			I	I					I I I I I I
MA SP									I I I I I	
LE HE				I I I I I I	I I I I	I I		I I		I I
AF EU	I I I I I I I I I I I I I I I I I			I	I					I I
AM				I I I I I I	I I I I I		I I	I I I I I I I I	I I I I I I
NL	C C C			D D	D D D D	B	B B B B B B	A	A	A A

FIG. 2. Dendrogram of 70 *Cyperus esculentus* plants representing the morphological variation of the studied vouchers. P.no. = population number according to Table 3. Variety according to Kükenthal (1935): ES = var. *esculentus*, CY = var. *cyclolepis*, NE = var. *nervoso-striatus*, MA = var. *macrostachyus*, SP = var. *sprucei*, LE = var. *leptostachyus*, HE = var. *heermannii*. Geographic origin: AF = Africa and Asia, EU = Europe, AM = N. and S. America, NL = the Netherlands. Biotypes A–D according to Ter Borg et al. (1988).
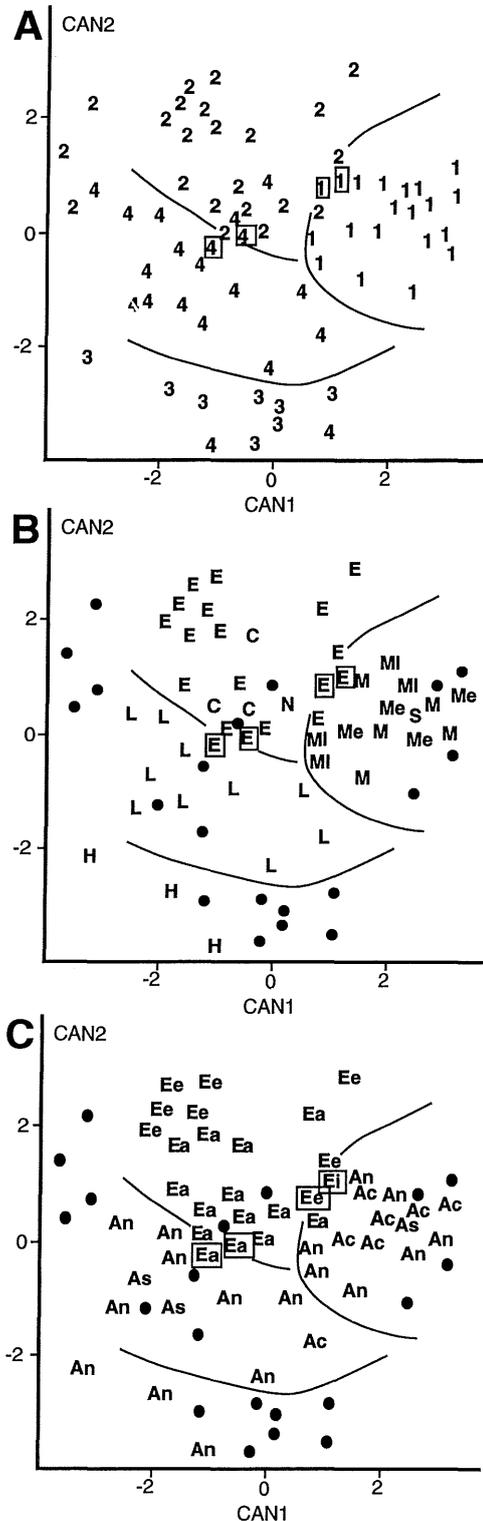
scales and spikelets of the var. *esculentus* and var. *leptostachyus* material of cluster 1, and the mean values of all plants of var. *esculentus*, var. *leptostachyus*, and var. *macrostachyus* measured. It indicates that the floral scale characters of var. *leptostachyus* and var. *esculentus* plants in cluster 1 are much more similar to the values observed in var. *macrostachyus* than to those found in both other varieties. Since floral scale characters were found to be more reliable than characters of spikelets, the plants concerned can be grouped together with var. *macrostachyus*. Plants belonging to the Dutch biotype A occur in this cluster.

Cluster 2 consists of 22 plants, all of these originating from the Old World (Africa, Europe, and Asia). The majority (16 plants) were identified as var. *esculentus*. Furthermore this cluster includes the type species of var. *nervoso-striatus* and var. *cyclolepis*. Figures 4A and B graphically present the characters measured and show a strong resemblance of the latter varieties to var. *esculentus*. This cluster includes biotype C from the Netherlands.

Cluster 3 includes eight plants. The two plants of var. *heermannii* are the only reference material from Kükenthal assigned to this cluster. Grouped with them are the Dutch biotype B plants except *De Nijs 7005* (WAG) (Table 3, no. 4).

Cluster 4 consists of 10 plants of var. *leptostachyus* and one of var. *heermannii*, all from the Americas, and two African plants of var. *esculentus*. The latter plants were already identified as var. *esculentus* because of their position in the ordination diagram and their determination by Kükenthal. With regard to its position in the ordination diagram (Fig. 3B) the plant of var.

←

FIG. 3. Ordination diagram of 70 selected *Cyperus esculentus* plants (first two canonical variables). A. Individual plants indicated by their cluster number in Fig. 2. B. Plants indicated by their variety according to Kükenthal (1935): C = var. *cyclolepis*; E = var. *esculentus*; H = var. *heermannii*; L = var. *leptostachyus*; M = var. *macrostachyus* (M_l and M_e were considered as var. *leptostachyus* and var. *esculentus* resp. by Kükenthal, 1935); N = var. *nervoso-striatus*; S = var. *sprucei*. C. Plants indicated by their geographic origin: A_n, A_c, A_s = North, Central and South America resp.; E_e = Europe, E_a = Africa, E_i = India. In B and C ● = plants from the Netherlands. Outlined plants are cases discussed in the text.

TABLE 5. Final determination of American *Cyperus esculentus* plants of cluster 1, which are erroneously determined by Kükenthal (1935), on floral scale and spikelet dimensions. Measurements (in mm) for G2, G4, G5, S4, and S6 are as described in Table 2 and Fig. 1. Population number according to Table 3. ES = var. *esculentus*, LE = var. *leptostachyus*, and MA = var. *macrostachyus*. Origin: Am = America, Af = Africa, Europe, Asia.

Population number	Number of plants	Determination Kükenthal (1935)	Origin	Floral scale			Spikelet		Final determination
				G2	G4	G5	S4	S6	
80	1	ES	Am	3.1	2.0	1.9	18.1	1.8	MA
84	1	ES	Am	3.0	2.1	1.5	12.2	1.7	MA
85	1	ES	Am	3.2	2.4	2.0	9.0	1.6	MA
86	1	ES	Am	3.2	2.3	2.0	12.0	2.4	MA
(Mean)	19	ES	Af	2.5	1.9	1.2	11.4	2.1	ES
(Mean)	5	MA	Am	3.3	2.1	1.6	37.8	2.5	MA
(Mean)	10	LE	Am	2.2	1.6	1.1	12.7	1.2	LE
73	1	LE	Am	3.1	2.1	1.5	22.0	1.7	MA
73	1	LE	Am	2.8	1.9	1.4	10.7	1.9	MA
79	1	LE	Am	3.5	1.9	2.0	17.0	1.7	MA
81	1	LE	Am	3.2	2.0	1.5	12.9	2.0	MA

heermannii might as well belong to cluster 3; the same holds for the one plant of the Dutch biotype B. Therefore cluster 4 appears to consist exclusively of var. *leptostachyus* and the six plants of biotype D, or nearly so.

DISCUSSION

Character Evaluation. Seventeen characters were selected as diagnostically useful for the infraspecific taxonomy, as opposed to seven characters used by Kükenthal (1935). Although not used by Kükenthal, dimensions of the floral scale (G10, G4 and G5), are significant characters according to the analysis of variance. Several characters mentioned by Kükenthal (1935) were not included in our analysis. Two were excluded because they were difficult to quantify (shape and color of spikelets) and four more characters, spikelet width (S6), number of spikelets per spike (E4), culm width (C7) and number of bracts (C8) were sensitive to environmental variation or shoot status (Table 4). Spikelet length (S4)

was left out because of its logical dependence on two other significant characters, S1 (number of floral scales on a spikelet) and S20 (number of floral scales/mm spikelet)

Spikelet length (S4) and width (S6) are the most important characters used by previous authors (Kükenthal 1935; Fernald 1950; Yip 1978) and are included in the descriptions of varieties and sometimes used for their delimitation. Usually exact values are given. According to the analysis of variance, spikelet length (S4) is a group 2 character. It differs significantly (P < 0.0001) between clones and between primary and secondary shoots (P < 0.001). For environmental conditions P was just over 0.01 (Table 4). Although spikelet length is a relevant character it may vary considerably within one clone (Fig. 5). According to Kükenthal (1935), varieties differ in spikelet lengths as follows: var. *esculentus* < 1.2 cm, var. *leptostachyus* and var. *heermannii* 1.5–2.0 cm, var. *sprucei* and var. *macrostachyus* up to 3.0 cm. Figure 5 shows that even plants of a single clone have spikelet

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FIG. 4. Characterization of varieties of *Cyperus esculentus* according to the 17 morphological characters measured. X-axis: mean values of all plants measured ± 2× s.d.; dotted area = mean values ± 1× s.d. (Dutch material not included). A. Var. *esculentus*; bold line indicates the type material of var. *cyclolepis* (*Rehmann 4776* [K]), average values of three plants on a sheet). B. Var. *esculentus*; bold line indicates the type plant of var. *nervoso-striatus* (*Burtt-Davy 9237* [PRE]). C. Var. *macrostachyus*; bold line indicates type plant of var. *sprucei* (*Spruce 6414* [K]). D. Var. *leptostachyus*. E. Var. *heermannii* (mean value of 3 plants).
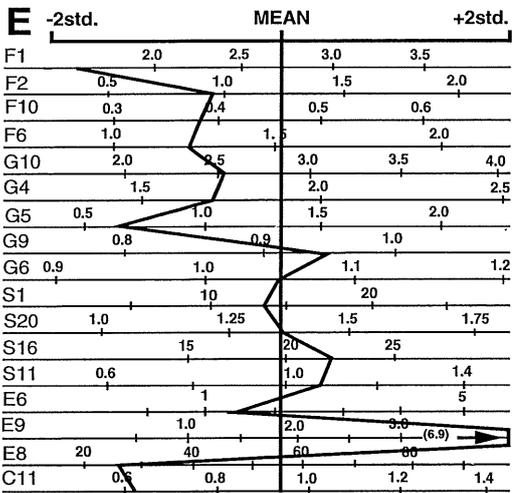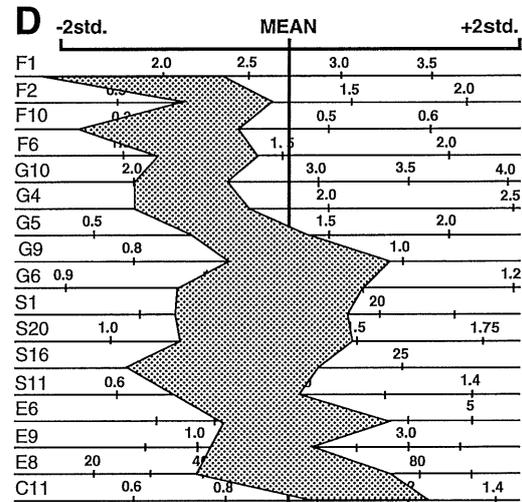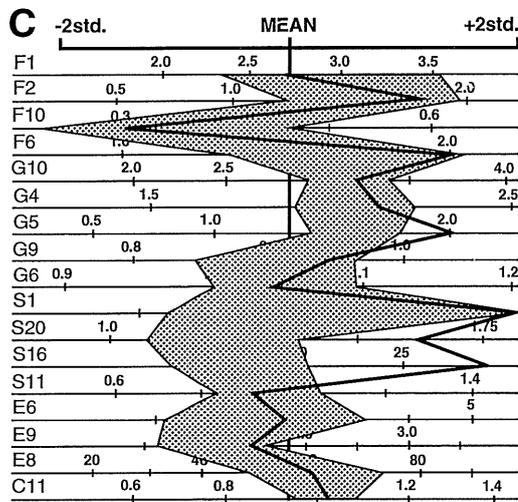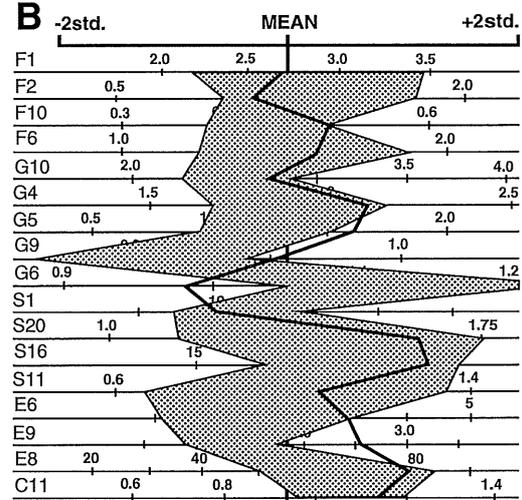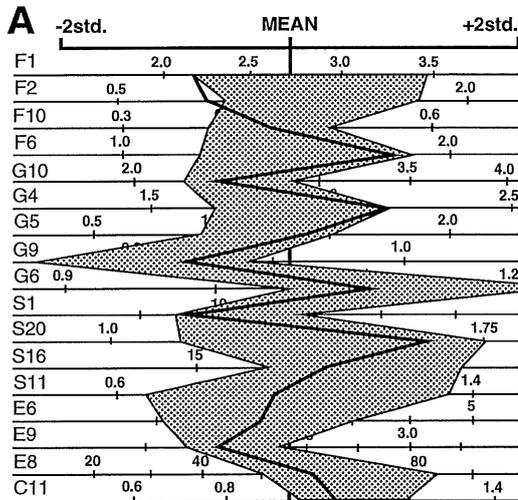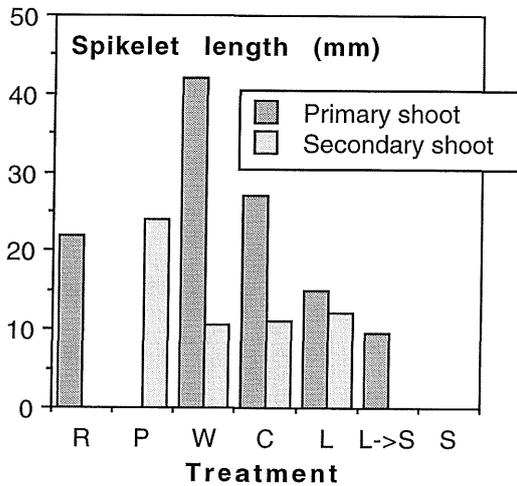
FIG. 5. Spikelet lengths in one clone of *Cyperus esculentus* (var. *macrostachyus*) plants grown under widely different conditions. If plants did not flower in a certain treatment no bar is drawn. Treatment conditions are those discussed in MATERIALS AND METHODS, where R = nitrogen rich, P = nitrogen poor, W = 22°C constant, C = 18°C constant, L = natural daylength in the Netherlands (long), L→S = natural daylength for one month changed to 12-hour cycles of light and dark for the remainder of the season, S = 12-hour cycles of light and dark during the entire growing season.

lengths in all categories. These results make the use of exact limits between varieties of this character questionable and give reason to doubt the central position of this character in the infraspecific taxonomy of Yellow Nutsedge.

Spikelet width (Table 2, S6) appeared to be sensitive to environmental conditions and no evidence of genetic differences between clones analyzed was found for this character. It is a product of length of floral scales (Table 2, G2) and angle of divergence of floral scales from the rachilla (Table 2, S16), both of which were selected as taxonomically useful characters. Spikelet width itself, however, is not a reliable character for the following reason. Plants analyzed often combined a long floral scale with a narrow angle of divergence, in which case spikelet width was normal (ca. 2 mm). Under relatively long dry conditions, however, scale angles increase slightly, with a strong effect on spikelet width, which is expressed as $2 \times \sin(\text{scale angle}) \times \text{scale-length}$. This strong effect is especially the case when scales are long and the

angle of divergence is normally narrow (e.g., in var. *macrostachyus*). Therefore spikelet width is an unreliable character, sensitive to drying and other environmental conditions (Table 4), and should not be used in assessing the infraspecific taxonomy of *C. esculentus*.

Treatment of the Varieties. The results of the numerical analysis show that all four clusters, after minor corrections, are homogeneous, in regard of morphology and geographic origin. They appear to correlate fairly well with taxa distinguished by Kükenthal (1935), who recognized them at the level of varieties. Later authors (e.g., Fernald 1950) reduced them to forms. However, because of the strong relationship between the clusters distinguished and their geographic origin (Fig. 3B, C) recognition at varietal level seems warranted. Moreover, it was found that populations differ with respect to a range of ecological, physiological, and agriculturally important characteristics. This variation appeared to be related to the taxa; therefore, following Kükenthal (1935) and Mohlenbrock (1960), we maintain a varietal classification.

In cluster 1 four varieties identified by Kükenthal are present. However, as indicated above, some of the plants included should be reclassified according to our standards. This leaves cluster 1 with var. *macrostachyus* and var. *sprucei*. Table 1 and Fig. 4C show that the differences between these varieties are very small. Originally var. *sprucei* was distinguished because of its longer stigmata, yellow-brown floral scales, and slightly wider spikelets (Table 1). However, Fig. 4C shows that all but two characters of the type specimen of var. *sprucei* (*Spruce 6414*) are within the range of variation of var. *macrostachyus*, the exceptions being floral scale density per spikelet (S20) and angle between floral scales and rachilla (S16). A further comparison of the type materials (*Spruce 6414* and *Drummond 452*) leads to the conclusion that there is little reason to distinguish two separate varieties. The fact that these have been distinguished may have a historical background. Variety *macrostachyus* was described in 1870, when Boeckeler reduced *C. lutescens* to varietal status within *C. esculentus*. Later Clarke (1884) introduced var. *sprucei*, for the American plants with large inflorescences. At that time he still considered *C. lutescens* as a distinct species. Since var. *macrostachyus* was the first variety de-

scribed, cluster 1 should have that name. This also means that, in contrast to Ter Borg et al. (1988), the Dutch biotype A should be identified as var. *macrostachyus*.

Cluster 2 includes three varieties, var. *esculentus*, var. *nervoso-striatus*, and var. *cyclolepis*. The latter was distinguished by Kükenthal (1935) because of its short and broad spikelets (Table 1); however, these characters were found to have a high level of plasticity. Since the type material (*Rehmann 4776*) hardly falls outside the central range of var. *esculentus* (Fig. 4A), we conclude that there is not enough evidence to consider var. *cyclolepis* varietally distinct. Plants identified as such belong to var. *esculentus*.

According to Kükenthal (1935), var. *nervoso-striatus* should be distinguished because of the deviating shape of its achenes and high spikelet density (Table 1). Figure 4B shows that achene width (F10) is rather high, but it is within the range of var. *esculentus*. Spikelet density (E9) is distinct, and relative length of the floral scales at the top and at the base of the spikelets (G6 and G9) have deviating values. However, the most important values of the flower and floral scale characters are well within the range of var. *esculentus*. Therefore, there is not enough reason to distinguish var. *nervoso-striatus* as a separate variety.

Though they are all in one subgrouping of cluster 2 (Fig. 3B), Dutch plants of biotype C fall within this cluster, and therefore also should be identified as var. *esculentus* instead of var. *cyclolepis* as was done previously (Ter Borg et al. 1988).

Cluster 3, apart from six plants of Dutch biotype B, includes only two plants identified as var. *heermannii*, viz., the type material (Table 3, no. 68). Several characters of these plants overlap with those of other varieties, especially with var. *leptostachyus*. However, inflorescences of plants in this cluster have a conspicuous habit (Fig. 6D), primarily due to an extremely high spikelet density (Fig. 4E). The number of rays is often much smaller than the number of involucral bracts (C11), indicating that some spikes did not develop. In the Netherlands, plants often did not flower at all, but produced a culm with bracts only (Fig. 6E). This might have been caused by some pathogen, as in *Cyperus virens* Michx., where a systemic fungus was found to induce vivipary (Clay 1986). However, the plants were found to differ in other respects also, e.g.,

density of the erect (E8) spikelets on the axis (E9), and shape and oil content of tubers (unpubl. data). This justifies recognition at the varietal level as var. *heermannii*. Further study of the Dutch plants indicated that more than one genotype is involved.

As discussed under RESULTS, cluster 4 retains only plants identified as var. *leptostachyus*, together with the Dutch biotype D (Fig. 4D). All others have been removed for the reasons discussed.

In general, the clusters distinguished herein correspond with taxa described in previous literature. In spite of the totally different starting points of the methods, these studies resulted in similar taxonomic patterns, yielding four varieties, var. *esculentus*, var. *leptostachyus*, var. *macrostachyus*, and var. *heermannii* described by Kükenthal (1935).

Geographic Distribution of the Varieties. Variety *esculentus* is widespread through Africa, India, and southern Europe, and var. *leptostachyus* dominates northern U.S.A and Canada and the southern parts of South America. In Central America var. *macrostachyus* is the common variety. Variety *heermannii* is rare, and restricted to the southwest of the U.S.A.

Kükenthal (1935) cited only 16 sheets of American var. *esculentus* plants, the four we determined proved to be var. *macrostachyus* plants, according to their floral scale morphology. This questions whether var. *esculentus* is common in the America's. Most of the American material we studied could be determined as var. *leptostachyus* and var. *macrostachyus*. However, the morphology of some plants remarkably resembles that of var. *esculentus*. The exact distribution of var. *esculentus* in the America's is therefore unknown but it is probably far more rare than var. *leptostachyus*, and its occurrence in the America's might be caused by introduction from Europe or Africa.

The occurrence of var. *leptostachyus*, var. *macrostachyus*, and var. *heermannii* in Europe is probably caused by recent introductions. Varieties *macrostachyus* and *heermannii* have restricted distributions in Europe, mainly in the Netherlands, which supports the hypothesis of their recent introduction from the America's as a contaminant of *Gladiolus* cormlings (Ter Borg and Schippers 1992; Rotteveel 1993). Variety *leptostachyus* is reported in several European countries and was probably introduced into
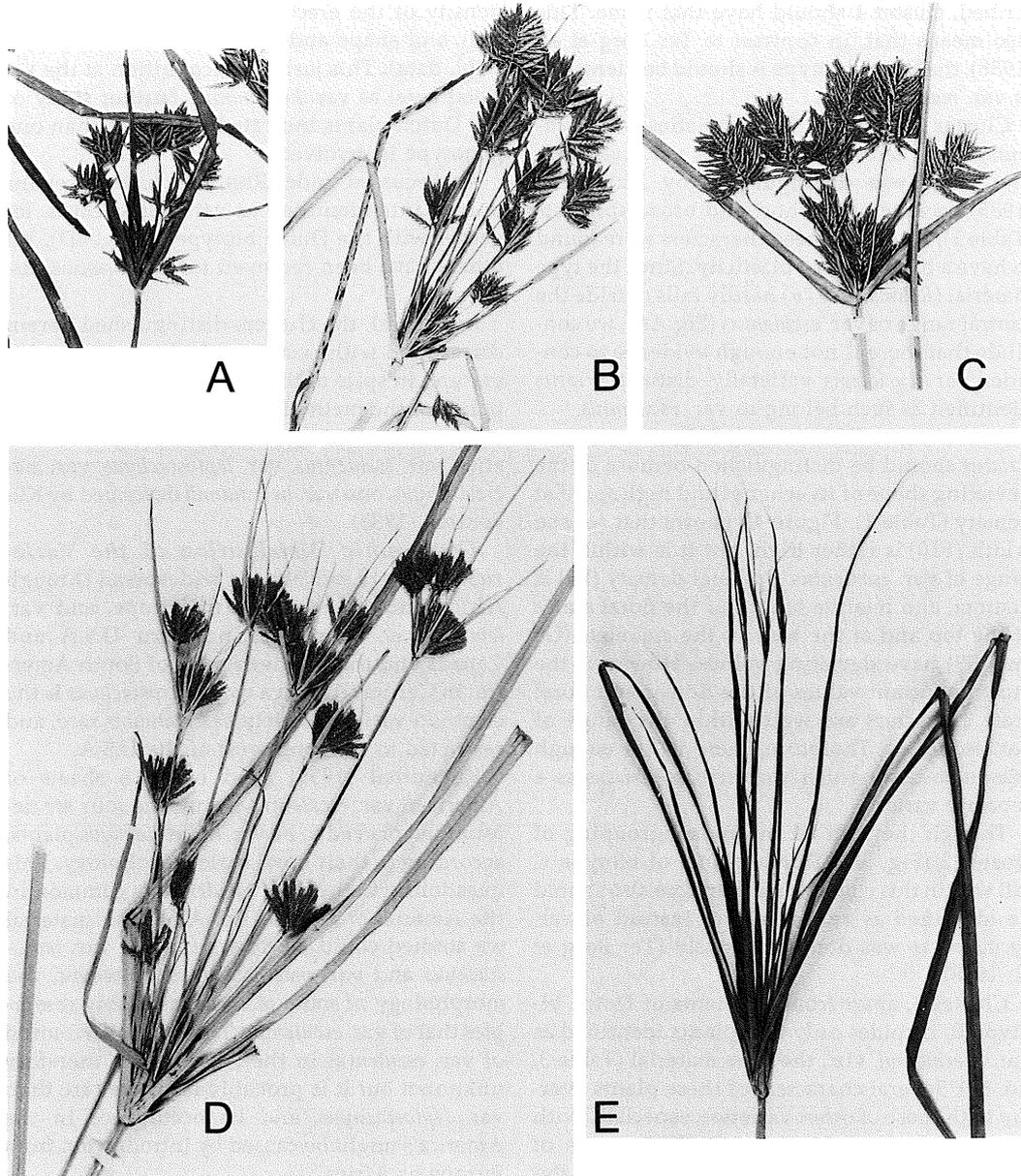
FIG. 6.   Habit of inflorescences of the accepted *Cyperus esculentus* varieties (⅓ of real size).   A. Var. *esculentus*, *Tisserant 1503* (K).   B. Var. *macrostachyus, De Nijs 6052* (WAG).   C. Var. *leptostachyus, Jörgensen 3575* (B).   D. Var. *heermannii, De Nijs 6910* (WAG).   E. Var. *heermannii, De Nijs 6712* (WAG).

France after the Second World War (Ter Borg and Schippers 1992). Variety *esculentus* appears to have remained within its original (southern) area of distribution in Europe (Ter Borg and Schippers 1992). Recent migrations imply that new contacts have been brought about between varieties that had been previously isolated. This may give rise to new genotypes, with intermediate morphology that can create new problems in the delimitation of the varieties.

Consequences of Plasticity. The plasticity of *C. esculentus* can have consequences for de-

termination of specimens. The effect of the environment can change the appearance of the plant drastically. Characters like spikelet length, width, ray length, bract length, and number of rays are all plastic. Since *C. esculentus* is a cosmopolitan species, this can easily lead to a wide range of morphological forms caused by interaction between environment and the different genotypes. This makes exact determination of varieties difficult, especially intermediates between var. *esculentus* and var. *leptostachyus*. Extreme forms of *C. esculentus* can look like closely related species, but *C. esculentus* is always characterized by the spherically shaped tubers, 0.3–1.5 cm in diameter, each individually developing at the end of a rhizome.

KEY AND TAXONOMIC TREATMENT

The following key to the accepted varieties of *C. esculentus* is based mainly on characteristics of individual flowers because the growing experiments indicated them as the most reliable parameters for segregation of the varieties.

1. Angle between spikelets and rachis (E8) < 35°, spikelet density on a spike (E9) > 2.0 per mm; ratio of number of rays to number of bracts (C11) < 0.75 or more than 15 flowers per spikelet .... var. *heermannii*
1. Other combination of characters.
　2. Mean floral scale length (G10) ≥ 3.4 mm .... var. *macrostachyus*
　2. Mean floral scale length < 3.4 mm.
3. Mean floral scale length (G10) ≥ 2.8 mm, and height where the floral scale reaches its maximum width (G5) ≥ 1.5 mm .... var. *macrostachyus*
3. Floral scale length < 2.8 mm and height where the floral scale reaches its maximum width (G5) < 1.5 mm.
　4. Mean floral scale length (G10) ≥ 2.5 mm, height where the floral scale reaches its maximum width (G5) ≥ 1.4 mm, maximum floral scale width (G4) > 1.8 mm; ratio of length of top floral scale to mean length of floral scales in the spikelet (G9) > 0.90 or number of floral scales per spikelet (S1) ≥ 20 .... var. *macrostachyus*
　4. Other combination of characters.
5. Length of style including branches (F1 + F2) ≥ 4.2 mm .... var. *esculentus*
5. Length of style including branches < 4.2 mm.
　6. Maximum floral scale width (G4) ≤ 1.5 mm .... var. *leptostachyus*
　6. Maximum floral scale width > 1.5 mm.

7. Number of floral scales per spikelet (S1) > 23 .... var. *leptostachyus*
7. Number of floral scales per spikelet ≤ 23.
　8. Ratio of top floral scale length to mean length of floral scales (G9) > 0.94 .... var. *leptostachyus*
　8. Ratio of top floral scale length to mean length of floral scales (G9) ≤ 0.94.
9. Maximum floral scale width (G4) ≤ 1.8 mm and length of style (F1 + F2) ≤ 3.4 mm .... var. *leptostachyus*
9. Maximum floral scale width > 1.8 mm and length of style > 3.4 mm.
　10. Maximum floral scale width (G4) ≤ 1.9 mm, mean floral scale length (G10) ≤ 2.3 mm and anther length (F6) ≤ 1.4 mm .... var. *leptostachyus*
　10. Higher character values.
11. Maximum floral scale width (G4) ≤ 2.0 mm, mean floral scale length (G10) ≥ 2.6 mm; length of style (F1 + F2) ≤ 3.5 mm or angle between floral scale and spikelet axis (S16) < 17° .... var. *leptostachyus*
11. Other combination of characters .. var. *esculentus*

After a general characterization of *C. esculentus*, descriptions are given for the four varieties accepted. These are primarily based on the clusters resulting from the numerical analysis and the parameters included. Ranges indicated are based on the average values plus or minus one standard deviation. Further details are given in Table 6. Relevant characters mentioned by other authors have been included, as far as their relation with the variety is consistent. This concerns characters of spikelets and tubers.

CYPERUS ESCULENTUS L. Sp. Pl. ed. 1: 45. 1753.—
　TYPE: Morison, Pl. hist. univ. vol. 3, sect. P, t. 11, no.8 ["10"], 1699, lectotype, designated by Tucker (1994).

Perennial often weedy plants with usually long fleshy rhizomes producing new shoots or with one persistent tuber at the end. Leaves 70(–120) cm long and up to 10 mm wide, linear, clustered, pale green. Culm up to 60(–100) cm long, triangular, ending in an inflorescence with 5–11, 10–50 cm long bracts around a number of spikes; the primary spike is almost sessile, the others are up to 25 cm long, usually half the length of the corresponding bract, pedunculate. Spikes, sometimes compound, with 2nd order branches, and up to 30(–50) spikelets. Spikelets compressed, 5–30(–55) mm long and 1–3 mm wide. Scales yellow-brown, (1.5–)2.0–3.3(–4.5)

TABLE 6. Mean values, standard deviation (s.d.) and minimum and maximum values observed in the varieties of *Cyperus esculentus* measured (Dutch plants not included). The underlined values indicate the most discriminating characters; see Table 2 for their more detailed description.

| Character desig-nation	var. *macrostachyus* N = 13				var. *esculentus* N = 19				var. *leptostachyus* N = 10				var. *heermannii* N = 3
	min.	mean	max.	s.d.	min.	mean	max.	s.d.	min.	mean	max.	s.d.	mean
F1	2.0	2.95	4.0	0.60	2.0	2.81	4.5	0.66	1.2	1.83	2.5	0.48	1.56
F2	0.9	1.64	2.2	0.36	0.6	1.37	2.2	0.43	0.7	0.99	1.2	0.18	0.93
F10	0.18	0.34	0.58	0.12	0.27	0.43	0.53	0.07	0.25	0.32	0.50	0.08	0.38
F6	1.2	1.69	2.1	0.33	1.0	1.57	2.1	0.32	1.0	1.26	1.6	0.17	1.23
G10	2.8	3.17	3.5	0.24	2.0	2.52	3.4	0.31	1.8	2.23	2.7	0.26	2.52
G4	1.8	2.09	2.4	0.17	1.6	1.93	2.4	0.25	1.5	1.62	1.9	0.16	1.70
G5	1.0	1.61	2.0	0.27	0.8	1.24	1.8	0.27	0.8	1.14	1.7	0.27	0.67
G9	0.79	0.90	1.00	0.05	0.66	0.80	0.93	0.07	0.83	0.92	1.01	0.06	0.95
G6	0.99	1.05	1.13	0.04	0.93	1.13	1.26	0.08	0.93	1.04	1.11	0.07	1.05
S1	6	21.6	42	13.6	6	11.4	19	4.0	5	12.7	20	5.4	13.3
S20	1.04	1.24	1.59	0.15	0.92	1.45	2.00	0.30	1.11	1.32	1.66	0.17	1.37
S16	13.0	17.4	23.0	3.4	15.0	22.5	28.0	4.3	11.0	16.3	24.0	4.1	22.0
S11	0.75	0.95	1.26	0.13	0.72	0.99	1.22	0.13	0.63	0.86	1.11	0.14	1.08
E6	0	1.8	4	1.5	0	1.6	4	1.4	0	2.3	3	1.32	1.33
E9	0.7	1.20	2.3	0.43	0.8	1.26	2.3	0.39	0.85	1.57	2.1	0.42	6.94
E8	40	61	80	14	40	67	90	17	30	55	80	18	26
C11	1.00	1.02	1.14	0.06	0.83	1.09	1.40	0.15	1.00	1.14	1.42	0.15	0.62
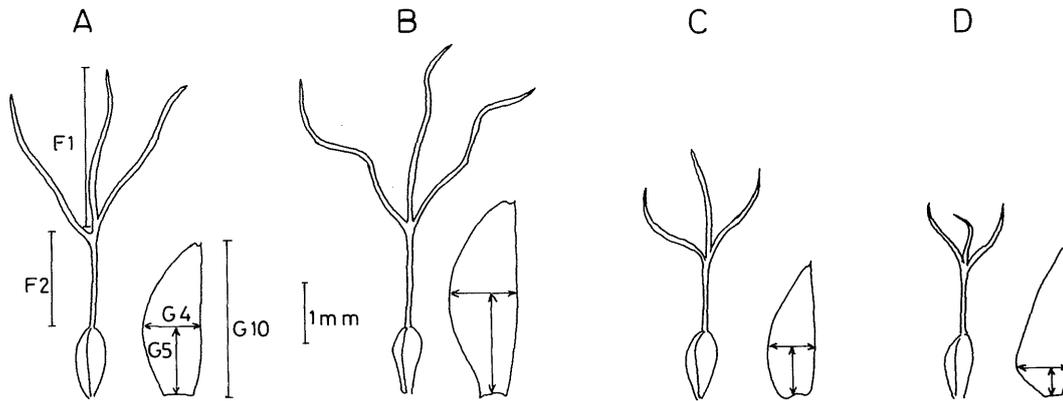
FIG. 7.   Characteristics of floral scales, ovaries, and styles of four *Cyperus esculentus* varieties according to average values of Table 6.   A. Var. *esculentus*.   B. Var. *macrostachyus*.   C. Var. *leptostachyus*.   D. Var. *heermannii*.

mm long and 1.4-2.4 mm wide, obtuse and sometimes slightly mucronulate, with 2-3 distinct veins, which can be reddish. Rachilla with adnate hyaline scales. Ovary 1-1.2 mm long and 0.3-0.6 mm wide, pale green. Achene 1.2-1.6 mm long and 0.5-0.8 mm wide, triangular, ellipsoid or narrowly obovoid, smooth, bright grey-brown. Anthers 1.0-2.1 mm long. Style (0.6-)0.8-2.0(-2.2) mm long, with three stigmata, length (1.2-)1.4-3.5(-4.5) mm.

CYPERUS ESCULENTUS L. var. ESCULENTUS

C. esculentus var. cyclolepis Boeck. ex Kük. (syn. nov., here designated), Kükenthal, Engl. & Diels, Pflanzenr. IV. 20: 119. 1935.—TYPE: S. Africa, Pretoria, *Rehmann 4776* (lectotype: B!, isolectotype:K!), *Thomas 113* (paratype: not seen).

C. esculentus var. nervoso-striatus (Turrill) Kük. (syn. nov., here designated), Kükenthal Engl. & Diels, Pflanzenr. IV. 20: 119. 1935. Basionym: *C. nervoso-striatus* Turrill, Kew Bull. 1925: 68. 1925.—TYPE: S. Africa, Ermelo; *Burtt Davy 9237* (holotype: PRE!).

Synonyms according to Kükenthal (1935): *C. aureus* Ten., *C. melanorrhizus* Delile, *C. hydra* Humb., Bombl. & Kunth, *C. nervosus*, Roem. & Schult., *C. tenorii* C. Presl, *C. tenorianus* Roem. & Schult., *C. sieberianus* Link, *C. pallidus* Savi, *C. damiettensis* A. Dietr., *C. retusus* Nees, *C. scirpoides* R.Br. ex Hochst., *C. buchananii* Boeck., *C. esculentus* L. var. *aureus* K. Richt., *C. fezelianus* C.B. Clarke, *Chlorocyperus aureus* Palla.

Tubers up to 10 mm long. Inflorescence sim-

ple to complex, rays usually with flowering spikes, and numerous (up to 2 per mm) flowers per spikelet. Spikelets 5-20 mm long and up to ca. 2 mm wide, sometimes short and then more or less obovoid. Flower size intermediate. Floral scales (2.0-)2.2-2.9(-3.4) mm long and (1.6-)1.7-2.2(-2.4) mm wide; their maximum width at (0.8-)1.0-1.5(-1.8) mm above the base. Anthers (1.0-)1.2-1.9(-2.1) mm. Style (0.6-)0.9-1.8(-2.2) mm long, stigma (2.0-)2.2-3.5(-4.5) mm. (Figs. 4A, B, 6A, 7A)

Distribution.   S. Europe, Asia and Africa; locally in northern areas of North America.

Vouchers.   Table 3 numbers: 50-67, 90 and *De Nijs 7020, 7415, 7417* (WAG).

CYPERUS ESCULENTUS L. var. MACROSTACHYUS Boeckeler, Linnaea 36: 291. 1870. Kükenthal, Engl. & Diels, Pflanzenr. IV. 20: 121. 1935.—TYPE: U.S.A., Texas, *Drummond 452* (holotype: B!; isotype: BM!, K!).

C. esculentus var. sprucei Clarke (syn. nov. here designated), J. Linn. Soc., Bot. 21: 181. 1884.—TYPE: Ecuador, Chanduy, *Spruce 6414* (holotype: K!).

Synonyms according to Kükenthal (1935): *C. lutescens* Torr. & Hook., *C. ruficomus* Buckley, *C. esculentus* var. *lutescens* (Torr. & Hook.) Kük.

Tubers up to 15 mm long (in the Netherlands). Inflorescence simple, rays usually with flowering spikes, many spikelets per spike. Spikelets up to 40 mm long and 3 mm wide. Large floral scales, (2.7-)2.9-3.4(-3.6) mm long

and (1.8-)1.9-2.3(-2.4) mm wide, at (1.0-)1.3-1.9(-2.0) mm from the base. Anthers (1.2-)1.3-2.0(-2.1) mm long. Style (0.9-)1.3-2.0(-2.2) mm long, stigma (2.0-)2.3(-4.0) mm long. (Figs. 4C, 6B, 7B)

Distribution. Southern parts of U.S.A., C. America; recently found in the Netherlands.

Vouchers. Table 3 numbers: 1, 5, 70, 71, 72, 73, 79, 80, 81, 84, 85, 86, 89.

CYPERUS ESCULENTUS L. var. LEPTOSTACHYUS Boeckeler, Linnaea 36: 290. 1870. Kükenthal in Engl. & Diels, Pflanzenr. IV.20: 119. 1935, excluding *Curtiss 3052* (US!, K!), *Ekman 14084* (K!), *Palmer 6454* (US!) all *C. esculentus* var. *macrostachyus.*—TYPE: U.S.A., Pennsylvania, *Willd. herb. no. 1377* (holotype: B-W, n.v., photo!).

Synonyms according to Kükenthal (1935): *C. phymatodes* Mühlenb., *C. tuberosus* Pursh, *C. nervosus* Bertol., *C. gracilis* Link, *C. repens* Elliott, *C. gracilescens* Roem. & Schult., *C. rotundus* Benth. non L., *C helodes* Schrad. ex Nees, *C. cubensis* Steud., *C. bahiensis* Steud. , *C. fulvescens* Liebm., *C. chrysostachys* Boeck., *C. esculentus* L. var *angustispicatus* Britton, *Chlorocyperus phymatodes* (Mühlenb.) Palla, *C. esculentus* L. var. *phymatodes* (Mühlenb.) Kük.

Tubers up to 10 mm long. Inflorescence simple, rays usually with flowering spikes. Second-order rays with up to 8 third-order rays. Spikelets 15-20 mm long and up to 1.5-2.0 mm wide. Flowers generally small; floral scales (1.8-)1.9-2.5(-2.7) mm long and 1.5-1.8(-1.9) mm wide, mucronate. Anthers (1.0-)1.3(-1.6) mm. Style (0.7-)1.0(-1.2) mm long, stigma (1.2-)1.8(-2.5) mm long. (Figs. 4D and 6C, 7C)

Distribution. N. and S. America, W. Europe (probably introduced around 1947).

Vouchers. Table 3 numbers: 3, 7, 74-78, 82, 83, 87, 88, and *De Nijs 7407 & 7418* (WAG).

CYPERUS ESCULENTUS var. HEERMANNII Torrey, Bot. Club XIII: 210. 1886. Kükenthal, Engl. & Diels, Pflanzenr. IV.20: 120. 1935. Basionym: *C. heermannii* Buckley, Proc. Acad. Sci. Philadelphia: 10. 1862, Boeckeler, Linnaea 36: 287. 1870.—TYPE: U.S.A., California, *Heermann 31882* (holotype: US!).

Tubers up to 10 mm. Inflorescence may be compound, with primary and secondary bracts at each level of branching, however, rays and flowers often do not develop, leaving the plants vegetative. Spikes with suberect (angle < 40°) spikelets close to each other on the rachis (> 2 per mm). Spikelets sometimes very long (up to 55 mm) and up to 3 mm wide. Flowers small, floral scales short, ca. 2.5 mm long and 1.7 mm wide, maximum width well below the middle of the floral scale; anthers 1.2 mm, style 0.9 mm and stigma 1.6 mm long. (Figs. 4E, 6D, E, 7D)

Distribution. South eastern parts of the United States; recently introduced into the Netherlands.

Vouchers. Table 3 numbers: 2, 68, 69, and *De Nijs 3540, 7005 & 7018* (WAG).

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