THE EVOLUTION OF GROWTH HABIT IN CYNODON L. C. RICH. (GRAMINEAE)

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ABSTRACT.—Vegetative characters studied included presence or absence of rhizomes, kind of rhizome, modification of stolon tips, branching patterns and winter hardiness. Growth habit, together with geographic distribution, ecological adaptation, and affinity based on cytogenetic studies suggests a sequence of evolutionary events in *Cynodon*.

A biosystematic study of the genus *Cynodon* was conducted at Stillwater, Oklahoma from 1963 to 1967 resulting in a revision of the genus (Clayton and Harlan 1970, Harlan and de Wet 1969, Harlan *et al.* 1969). The species and varieties as now recognized are presented in Table 1.

TABLE 1.—The Species and Varieties of *Cynodon*.

Epithet	2n Chromosome Number	Distribution
C. aethiopicus Clayton et Harlan	18, 36	East Africa; Ethiopia to Transvaal
C. arcuatus J. S. Presl ex. C. B. Presl	36	Malagasy, Ceylon, India, Southeast Asia, Philippines, Taiwan, Indonesia to Australia
C. barberi Rang. et Tad.	18	South India
C. dactylon (L.) Pers		
var. *dactylon*	36	Cosmopolitan
var. *afghanicus* Harlan et de Wet	18, 36	Afghanistan
var. *aridus* Harlan et de Wet	18	South Africa to Palestine to South India; intro. in Hawaii, Arizona
var. *coursii* (A. Camus) Harlan et de Wet	36	Madagascar
var. *elegans* Rendle	36	Southern Africa; Mozambique, Zambia and Angola southward
var. *polevansii* (Stent) Harlan et de Wet	36	Baberspan, South Africa
C. incompletus Nees		
var. *incompletus*	18	South Africa
var. *hirsutus* (Stent) Harlan et de Wet	18, rarely 36	South Africa
C. nlemfuensis Vanderyst		
var. *nlemfuensis*	18, rarely 36	Tropical Africa; Ethiopia to Zambia, west to Angola
var. *robustus* Clayton et Harlan	18, 36	East Africa; Ethiopia to Rhodesia
C. plectostachyus (K. Schum.) Pilger	18	Ethiopia, Uganda, Kenya, Tanzania
C. transvaalensis Burtt-Davy	18	Transvaal and Orange Free State

Specimens were examined at Kew, British Museum, Paris, Brussels, Berlin, Florence, Geneva, Honolulu, Bangkok, Manila, Los Banos, and Washington. The revised classification, however, was based primarily on a living collection of some 700 accessions grown in uniform nurseries at Stillwater. In the living material, it was noted that most of the taxa could be distinguished by characteristic growth habits. Vegetative characters are difficult to describe and are highly subject to environmental modification, yet they are useful for field identification and have evolutionary implications. They tend to go unnoticed in the herbarium because few specimens are sufficiently complete to reveal growth characteristics. The main types of growth habits are described in this paper as an aid to identification and to shed some light on evolution in the genus.

Description

RHIZOMES: The genus is essentially caespitose; only *C. transvaalensis* and four of the six varieties of *C. dactylon* have rhizomes. There are, however, two kinds of rhizomes, Fig. 1. One tends to be relatively slender, straight, with long internodes and the tip always stays below the surface. Lateral buds grow upward and emerge to form culms, but the rhizome itself remains underground, Fig. 1A. The other kind of rhizome is relatively large in diameter, fleshy, usually crooked with short internodes and the tip may grow to the surface where the rhizome is converted into a stolon, Fig. 1B. The first type grows faster and deeper than the second. The distribution of rhizome types is given in Table 2.

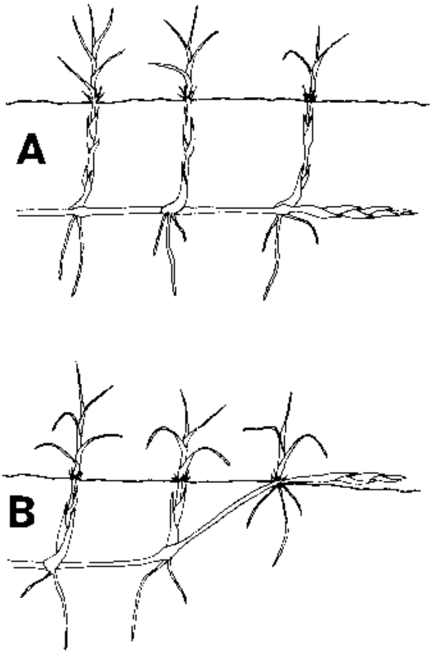

FIGURE 1. Two types of rhizomes in *Cynodon*.
- *A.* A true rhizome in which the tip always stays below the soil surface.
- *B.* Rhizome that emerges and is converted to a stolon.

The inheritance of rhizome formation was studied in a limited number of the hybrids produced in the course of the biosystematic study, Table 3. In hybrids between nonrhizomatous and rhizomatous species, rhizome formation was suppressed, but the nonrhizomatous varieties of *C. dactylon* were not able to suppress rhizome formation. The tetraploid race of *C. nlemfuensis* var. *robustus* does not suppress rhizomes completely, and, indeed, rhizomes were produced in hybrids between it and

TABLE 2.—Some Characteristics of Growth Habit in *Cynodon*.

Taxon	Rhizome Type (Fig. 1)	Stolon Tip (Fig. 2)	Stolon Branching (Fig. 4)	Turf Formation	Size*	Tissue Hardiness
C. aethiopicus	None	A	A	Very Open	Large	None
C. arcuatus	None	A	A	Open	Small	None
C. barberi	None	A	A	Open	Small	None
C. dactylon						
var. *dactylon*	A & B	A, R, B	B, C	Dense	Small-Medium	Variable
var. *afghanicus*	None	A	A	Very Open	Medium	Yes
var. *aridus*	A	A	A	Open	Small-Medium	None
var. *coursii*	None	R	B	Dense	Large	None
var. *elegans*	B	B	A	Lax	Medium	None
var. *polevansii*	A	B	C	Dense	Small	Yes
C. incompletus						
var. *incompletus*	None	R	B	Dense	Small	Yes
var. *hirsutus*	None	R	B	Dense	Small	Yes
C. nlemfuensis						
var. *nlemfuensis*	None	A	A	Open	Medium-Large	None
var. *robustus* (2x)	None	A	A	Very Open	Large	None
var. *robustus* (4x)	None	A	C	Open	Large	None
C. plectostachyus	None	A	B	Open	Large	None
C. transvaalensis	B	B	B	Dense	Small	Yes

*** Small plants are usually less than 15 cm tall; large plants are usually over 40 cm tall under nursery conditions.**

TABLE 3.—Rhizome Formation in Hybrids Between Nonrhizomatous and Rhizomatous Taxa

Nonrhizomatous Parent	Rhizomatous Parent	Number Hybrids Examined	Rhizome Formation
C. aethiopucus (4x)	*C. dactylon* (4x)	4	—
C. incompletus (2x)	*C. dactylon* (2x)	3	—
C. incompletus (2x)	*C. dactylon* (4x)	65	—
C. nlemfuensis var. *nlemfuensis* (2x)	*C. dactylon* (2x)	35	—
C. nlemfuensis var. *nlemfuensis* (2x)	*C. dactylon* (4x)	22	—
C. nlemfuensis var. *robustus* (2x)	*C. dactylon* (2x)	4	—
C. nlemfuensis var. *robustus* (4x)	*C. dactylon* (4x)	15 + 4*	—
C. dactylon var. *afghanicus* (2x)	*C. dactylon* (2x)	35	+
C. dactylon var. *afghanicus* (2x, 4x)	*C. dactylon* (4x)	47	+
C. dactylon var. *coursii* (4x)	*C. dactylon* (2x)	41	+
C. dactylon var. *coursii* (4x)	*C. dactylon* (4x)	43	+
C. dactylon var. *coursii* (4x)	*C. transvaalensis* (2x)	6	+

*** Four F_1 plants of this combination had short, poorly developed rhizome-like structures.**

tetraploid *C. dactylon* var. *afghanicus.* The fact that nonrhizomatous parents could produce rhizomatous offspring suggests that both parents carried recessive genes for rhizome production. Our collection also contained populations of *C. dactylon* var. *coursii* that apparently had already crossed with var. *dactylon* in Madagascar and segregated for rhizome production in our nurseries. The character gives every evidence of being rather simply inherited.

STOLON TIPS: There are striking differences among taxa in the morphology and behavior of stolon tips. Two extremes are shown in Fig. 2. In one kind, the tips are soft and leafy and the blades, when fully developed, are little different from those of the culms, Fig. 2A. In the other type, the blades are reduced to small flaps and the encasing sheaths are hardened, producing a sharp organ capable of penetrating soil, Fig. 2B. The organ resembles the penetrating tip of a rhizome, and, in fact, is readily converted into a rhizome when buried in the soil. Stolons with leafy tips simply stop growing when buried.

In some races of *C. dactylon* var. *dactylon,* the stolons regularly bury themselves, pushing the sharp tips down into the soil where the stem is converted to a rhizome which may emerge again after a short distance to be reconverted into a stolon. The horizontal stems of these plants seem to ''gallop'' alternately plunging into the soil and emerging again, producing rhizomes and stolons alternately along the length of the stem.

The extremes, as figured, are easily recognized, but there are intermediate forms that are very difficult to classify, especially with herbarium specimens. In *C. incompletus,* for example, the blades of the stolon leaves near the tip are much reduced and they never develop as fully as the leaves on the culm. The stolon tip may resemble the sharp-pointed organ just described, but it is softer and cannot be converted into a rhizome by burial in the soil. In Table 2, we have listed such intermediates as ''R'' for the reduced blades of stolon leaves. *C. dactylon* var. *dactylon* is especially variable and all

FIGURE 2. Stolon tips.
A. Leafy type relatively unmodified.
B. Extreme of modified type in which the sheaths are hardened and the blades much reduced.

classes of stolon tips are found in it.

BRANCHING HABIT: Branching patterns depend on the number and position of buds differentiated and on the timing of their development. In most grasses, leaves are arranged alternately in two ranks on the culm, one leaf to the node and each subtending a lateral bud in the axil. In *Cynodon* and some other grasses the culms have two leaves at each node, but only the lower subtends a lateral bud (Bogdan 1952). If the nodes were truly compound, one would expect each leaf to subtend a bud. The culm nodes could be interpreted as simple with the upper leaf subtending the terminal bud even though the terminal bud becomes far removed by subsequent growth of the culm, Fig. 3A. The lateral bud is usually suppressed, although those at the base of the culm may develop into a branch if the culm is allowed to develop fully.

The stolon nodes of *Cynodon* are compound and have three leaves, the lower two subtending lateral buds on opposite sides of the stolon, Fig. 3B. In some taxa, notably races of *C. dactylon* var. *dactylon,* the stolon nodes appear to have more than three leaves, but careful examination of young nodes near the tip shows that the basic ground plan is essentially constant. The additional leaves are derived from precocious growth of the lateral buds.

Of the two buds, the lower one is the first to grow and develop into either a stolon branch or a culm. Growth of the upper bud may be suppressed for a long time resulting in a stolon with conspicuously alternate branching, Fig. 4A. In such

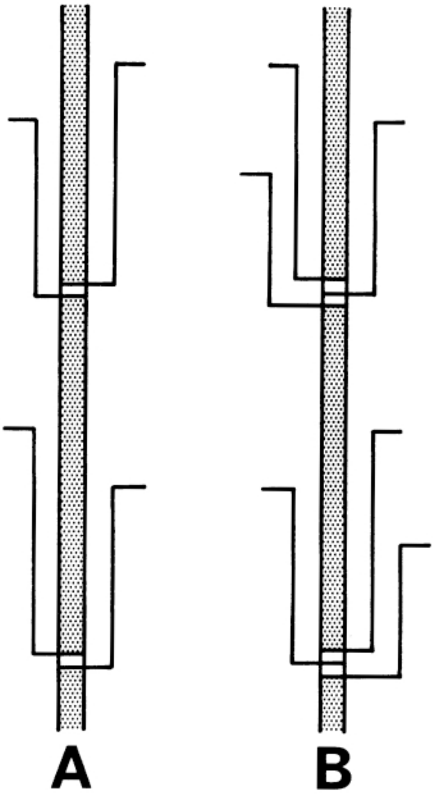

FIGURE 3. Diagram of culm leaves, *A* and stolon leaves, *B.*

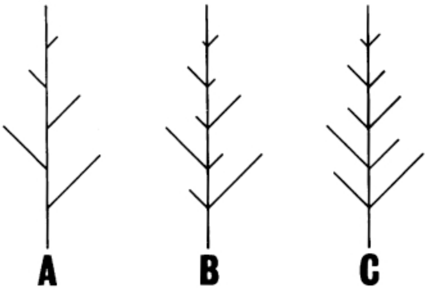

FIGURE 4. Branching patterns.
A. Alternate, one bud suppressed.
B. Intermediate, one bud delayed.
C. Opposite subequal.

stolons, rooting is usually also suppressed so that in the larger forms, one may lift up a stolon one or two meters long unattached to the soil, and with regular alternate branches down its length. Under natural conditions, stolons of this type may festoon shrubs and even small trees three meters or more in height. They tend to have long internodes ($>$ 10 cm and sometimes $>$ 20 cm) and are very fast growing. Under nursery conditions they may grow 10 meters or more in a single season. Plants of this type produce a loose, open mat of growth rather than a dense turf.

At the other extreme, are taxa in which the upper bud at a node develops almost immediately after the lower one, producing a branching pattern that appears to be opposite and subequal, Fig. 4C. These tend to have short internodes, root freely, and form a dense turf covering the soil almost completely. Furthermore, the branches themselves branch quickly and nodes only a short distance back from the tip may show a knot of growth consisting of several culms, short stolon branches, and many leaves. In the absence of competition, the turf creeps in a closed, dense front across the soil surface, rooting immediately behind the stolon tips.

Again, the two extremes are conspicuously different, but some taxa show intermediate behavior as in Fig. 4B. An individual plant may also be rather variable. During periods of maximum growth, internode elongation is sufficiently rapid that the branching appears alternate, but as growth slows down the development of the two buds at a node become more nearly synchronous and the branching approaches opposite. The upper latera' bud usually grows eventually even in forms that have a distinctly alternate branching pattern. Despite the variability, branching habits of some taxa are conspicuously different from others. *Cynodon aethiopicus, C. nlemfuensis* var. *nlemfuensis* and 2x var. *robustus, C. arcuatus, C. barberi* and *C. dactylon* var. *aridus, afghanicus* and *elegans* have consistently alternate branching, at least along the distal portions of the stolons. *Cynodon plectostachyus, C. nlemfuensis* var. *robustus* (4x), *C. incompletus, C. transvaalensis,* and *C. dactylon* vars. *dactylon, coursii,* and *polevansii* have essentially opposite branching patterns.

SIZE: There are striking differences among taxa with respect to plant size. This, again, is a variable character and readily influenced by environment. Under conditions of a uniform nursery in full sunlight and with competition with other vegetation removed, the differences are so consistent that plant size is one of the most conspicuous of all characters. Under these conditions, small plants are usually 15 cm or less in height and large plants are generally 40 cm or more. Some of the most robust forms may exceed a meter in height. A rough classification of plant size is presented in Table 2.

HARDINESS: *Cynodon* is basically a tropical genus and plants of most species are very sensitive to freezing. Plants of *C. arcuatus, C. barberi, C. aethiopicus, C. plectostachyus, C. nlemfuensis, C. dactylon* var. *coursii* and some races of var. *dactylon* are completely destroyed by a killing frost under Oklahoma conditions. *C. dactylon* var. *aridus* apparently has no tissue hardiness, but can usually overwinter at Stillwater by virtue of the deep rhizomes that escape killing temperatures. *C. dactylon* var. *elegans* has the same faculty, but the rhizomes do not go as deep and mortality is very high. Plants of the tropical race of var. *dactylon* may survive especially mild winters, but always with very severe injury. Deep rhizomes can act as a survival mechanism for plants without tissue hardiness.

Cynodon incompletus and *C. dactylon* var. *afghanicus*, on the other hand, have good tissue hardiness but no rhizomes. Both overwinter well in Oklahoma. *Cynodon transvaalensis*, *C. dactylon* var. *polevansii* and many accessions of var. *dactylon* have both tissue hardiness and rhizomes.

LEAF SHAPE: Three species can be easily recognized by leaf shape. In *C. barberi*, the leaves are broadly ovate-lanceolate, conspicuously different from all other taxa in the genus. In *C. arcuatus*, the leaves are broadly linear-lanceolate, rather intermediate between *C. barberi* and most of the other taxa. There is no overlap, however, and the leaves of *C. arcuatus* are readily recognizable. *Cynodon transvaalensis* represents the other extreme, with slender linear leaves finer than in any other species in the genus. Plants of all other taxa have linear-lanceolate leaves more or less alike in form. There is a conspicuous range in size, but only the three species mentioned can be consistently distinguished by leaf shape.

INTERPRETATION

Cynodon barberi and *C. arcuatus* are well separated from the rest of the genus not only by leaf shape and growth habit, but by inflorescence and spikelet characters and by genetic barriers (Harlan and de Wet 1969, Harlan *et al.* 1969). The distribution of *C. arcuatus* across the islands of the Indian and South Pacific Oceans from the Comoros and Seychelles to Australia suggests an ancient distribution of ancestral forms, clearly distinct from the geographic patterns of the rest of the genus. *Cynodon barberi* shows some morphological affinity to the nearest genus, *Brachyachne*, which is represented by a number of species in both tropical Africa and Australia that were at one time assigned to *Cynodon*. *Cynodon barberi* and *C. arcuatus* appear, therefore, to represent a very early differentiation from the ancestral *Cynodon* stock and are no longer closely related to the remaining taxa.

A second clearly separable group includes the large East African species *C. aethiopicus*, *C. nlemfuensis*, and *C. plectostachyus*. They share a number of growth habit characteristics such as lack of rhizomes, leafy stolon tips, lack of hardiness, large size, open growth and mostly alternate branching patterns. All three have distributions closely associated with the Great Rift Valley. In crossability studies reported by Harlan *et al.* (1969), it was shown that *C. plectostachyus* is completely isolated genetically from other taxa and that *C. aethiopicus* is isolated by very strong genetic barriers.

A third natural group includes the South African endemics, *C. incompletus* and *C. transvaalensis.* They are small, turf-forming diploids with far more winter hardiness than is required by their present habitats in South Africa. Although sympatric in part, they do not seem to cross in nature, but can be hybridized artifically (Harlan *et al.* 1970).

In the complex species *C. dactylon,* there is nothing that appears directly related to the first group. *C. dactylon* var. *coursii,* however, is a large, tropical, nonhardy and nonrhizomatous form with evident connections to *C. nlemfuensis.* Harlan *et al.* (1969) report that it crosses rather easily with other varieties of *C. dactylon* and that some hybrids with *C. nlemfuensis* were produced. The variety *polevansii* is a small, turf-forming, winterhardy endemic of South Africa evidently associated with the third group. The other African variety, *elegans* has growth habits that suggest it is a tetraploid form derived, in part at least, from the diploid var. *aridus.*

Finally, the Asian forms of *C. dactylon* seem to form a fourth group. Harlan and de Wet (1969) have shown that var. *aridus,* var. *afghanicus,* and the winterhardy temperate races of var. *dactylon* interact genetically in Asia. Introgression between hardy races of var. *dactylon* and hardy var. *afghanicus* is especially evident in Afghanistan. There is no apparent genetic connection between the winterhardy forms of Asia and those of South Africa. Hardiness has evolved independently in two widely separated regions. Furthermore, it is the Asian group that has produced the cosmopolitan weed var. *dactylon* (Harlan and de Wet 1969).

We, therefore, postulate the following sequence of evolutionary events:

1). *C. barberi* and *C. arcuatus* separated early from the remainder of the *Cynodon* stock. They are different morphologically, completely isolated genetically, and have distributions and affinities that suggest an early differentiation. Croizat (1968) assigns distributions of this type to precretaceous events.

2). The large, robust forms of East Africa (*C. aethiopicus, C. nlemfuensis, C. plectostachyus*) evolved, adapted to rather high rainfall and warm temperatures. Their distributions are closely associated with the Great Rift Valley and adjacent highlands which began to assume their present conformation in mid-Tertiary.

3). A diploid form evolved rhizomes and invaded the more arid regions of Africa, the Near East, and India. There were both small and large races and *C. dactylon* var. *aridus* represents the modern survivor of the progenitor rhizomatous *C. dactylon.*

4). The South African endemics evolved in isolation from the rhizomatous forms of India and the Near East. Winterhardy forms, with and without rhizomes, emerged more or less simultaneously in South Africa (*C. incompletus, C. transvaalensis*) and in Asia (*C. dactylon* var. *afghanicus* and var. *dactylon*). The high degree of winterhardiness in the South African species implies natural selection and survival through the Pleistocene.

5). *C. dactylon* var. *dactylon,* in part through genetic interaction with var. *afghanicus* and var. *aridus* became a cosmopolitan weed (Harlan and de Wet 1969). The high degree of winterhardiness of the temperate races of this variety also implies a Pleistocene evolution, but the cosmopolitan distribution, especially in the Pacific Islands and the New World is a recent historical phenomenon.

SUMMARY

Although highly subject to environmental modification, the vegetative characters in the genus *Cynodon* are useful for field identification and have evolutionary implications. Detailed observations of growth habit and characteristic features of rhizomes and stolons are described.

The genus is essentially nonrhizomatous; only *Cynodon transvaalensis* and four of the six varieties of *C. dactylon* have them. In some taxa, the rhizomes and stolons are interconvertible; others have true rhizomes and true stolons that are not convertible.

The compound nodes of stolons have three leaves, each subtending a bud, one terminal and two lateral. Of the two lateral buds, the lower one grows first and develops into either a stolon or a branch. The second bud grows after a delay of varying duration. The length of the delay accounts for the branching patterns of stolons.

A sequence of evolutionary events in *Cynodon* has been postulated after taking into account the information available from geographic distribution and cytogenetic studies.

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LITERATURE CITED

BOGDAN, A. V. 1952. Observations on stoloniferous grasses in Kenya. J. East Afr. Nat. Hist. Soc. 20: 71-76.

CLAYTON, W. D. and J. R. HARLAN. 1970. The genus *Cynodon* L. C. Rich. in Tropical Africa. Kew Bull. 24: 185-189.

CROIZAT, LEON. 1968. Introducion raisonee a la biogeographie de l'Afrique. Mem. Soc. Brot. Vol. 22, Coimbra.

HARLAN, J. R. and J. M. J. DE WET. 1969. Sources of variation in *Cynodon dactylon* (L.) Pers. Crop Sci. 9: 774-778.

RICHARDSON, W. L. 1969. Hybridization studies with species of *Cynodon* from East Africa and Malagasy. Amer. J. Bot. 56: 944-950.

————————, M. R. FELDER, K. M. RAWAL and W. L. RICHARDSON. 1970. Cytogenetic studies in *Cynodon* L. C. Rich, (Gramineae). Crop Sci. 10: 288-291.

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