

The taxonomic position of C_3 and C_4 *Alloteropsis semialata* (Poaceae) in southern Africa

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ABSTRACT

Alloteropsis semialata (R. Br.) Hitchc. sensu Chippindall (1955) and Clayton (in press) is the only known grass species in which elements with both non-Kranz and Kranz leaf blade anatomy, and therefore with C_3 and C_4 photosynthetic pathways are included. In the past, two taxa had been recognized, but the characters used to separate them were found to be unreliable, so they were united. However, study of voucher specimens for anatomical and physiological work has shown that C_3 and C_4 taxa may be separated on the basis of morphological characters that differ from those considered in the past. Therefore, two taxa are again recognized, this time at the rank of subspecies, and the name *Alloteropsis semialata* subsp. *eckloniana* (Nees) Gibbs Russell *stat. nov.* is published.

INTRODUCTION

Alloteropsis semialata (R. Br.) Hitch. is a grass of common, though never dominant, occurrence in the grasslands and open woodlands of the eastern part of southern Africa. Acocks (1975) reports it as an important constituent of 13 veld types. Its worldwide distribution extends from southern and tropical Africa to India, China, the Philippines and Australia.

Ellis (1974a, 1974b) has shown that the species as accepted by Chippindall (1955) and Clayton (in press) has both non-Kranz and Kranz leaf anatomy, and therefore has C_3 and C_4 photosynthetic metabolism. Frean & Cresswell (1979), Frean, Barrett & Cresswell (1980) and Ellis (1981) report the physiological features of C_3 and C_4 individuals in details and give additional differences in plant morphology and epidermal anatomy.

A. semialata is the only known grass which has both C_3 and C_4 metabolic forms. In the Poaceae, either pathway is normally characteristic at the taxonomic levels of subfamily and tribe, but two subfamilies, the Panicoideae and Arundinoideae, have both pathways. All the genera in Paniceae (*s.l.*) are either C_3 or C_4 except *Panicum*, *Neurachne* and *Alloteropsis*, but within *Panicum* and *Neurachne* (Hattersley, Watson & Johnson, 1982) individual species are either C_3 or C_4 . In *Alloteropsis* alone is there a species recognized that exhibits both anatomical types and both physiological processes (Ellis, 1974a).

The aim of this paper is to show that the C_3 and C_4 anatomical/physiological forms are supported by vegetative characters that do not intergrade in southern Africa, and which differ from characters used previously to separate entities in the species. The two forms are recognized as subspecies.

HISTORICAL BACKGROUND

In the past, two entities which are currently combined in *A. semialata* (R. Br.) Hitchc. have been

recognized, one with long racemes with loosely-placed, pale spikelets, and the other with short racemes with tightly-packed, very dark spikelets. The variants and the intergradation between them have been treated in several ways in the past.

Nees was the first to deal with both entities. In 1833 he created a new genus, *Coridochloa*, and transferred to it *Panicum semialatum* R. Br., which had been described by Robert Brown in 1810 on the basis of a specimen from Carpentaria in Australia. In 1834, Nees described a new monotypic genus *Bluffia eckloniana*, based on specimens collected by Drège at Katberg and Port Natal. Nees therefore considered that the two entities belonged to different genera.

By the end of the century, the taxa were better known over their large range, and they were seen to be more closely related. Hackel (1894) reduced *Bluffia eckloniana* to a variety of *Panicum semialatum*. Two years later, working on specimens from India, Hooker (1896) moved *Panicum semialatum* to the genus *Axonopus*. Stapf (1899) in *Flora Capensis* followed the generic placement of Hooker and the varietal placement of Hackel, and called the South African plants *Axonopus semialatus* (R. Br.) Hook. f. var. *ecklonii* Stapf, but treated the variety name as 'new'.

The current generic placement of the taxa was effected by Hitchcock (1909) when he recognized that the type specimen of Presl's (1830) genus and species *Alloteropsis distachya* was identical to *Panicum semialata* (Nees) Hitchc. (Chase, 1911). He did not at that time transfer Nees's southern African entity to the new genus, but in 1916 published the new combination *A. eckloniana* (Nees) Hitchc., therefore evaluating the differences between the two taxa at the specific level.

Stapf (1919) in *Flora of Tropical Africa* followed Hitchcock's acceptance of Presl's genus, but again treated the southern African taxon as a variety, *A. semialata* (R. Br.) Hitchc. var. *ecklonii* (Stapf) Stapf, once more using his own epithet '*ecklonii*'.

More recently, variation within the species has not been given taxonomic status. Phillips used only the name *A. semialata* and did not recognize a variety. Chippindall (1955) stated specifically that

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the variety (*'ecklonii'*) should be disregarded because the range of variation was so wide that the characters were not diagnostic. Clayton (in press) has adopted the same course for the Flora of Tropical East Africa. He says that the southern African variety is of limited taxonomic significance, because it merges completely with the rest of the species. He mentions the anatomical differences found by Ellis (1974a, 1974b), but does not comment on their taxonomic value.

During this long history of changes in interpretation, the two have been treated as different genera, different species and different varieties. They have most recently been reduced to a single variable species, when it became clear that the 'Australian' form also occurred in southern Africa, and that the criteria originally used to separate the taxa, mainly raceme colour, density and length, were variable and did not serve to separate the taxa adequately. An unfortunate result was that when anatomical and physiological investigations showed great differences within the species, there was no way to deal with the differences taxonomically at that time, because the infraspecific taxa had already been rejected on other grounds.

SEPARATION OF THE TAXA USING ANATOMICAL AND VEGETATIVE CHARACTERS

Re-evaluation of the variation within *A. semi-alata*, taking into account the anatomical differences that are indicators of different pathways, was possible because Ellis made over 50 voucher specimens for which determination of C_3 (non-Kranz) or C_4 (Kranz) anatomy had been carried out. These specimens were scored for a number of characters: length of longest raceme, spikelet colour, shape of leaf tip, width of leaf blade, hairiness of leaf blade, outline shape of basal parts, width of veins in basal sheath, length of hairs on basal sheath, and splitting of basal sheath into fibres. Fig. 1 shows the characters finally used to illustrate variation between the forms. The first analysis of this data showed that Chippindall and Clayton were correct in discounting raceme length and spikelet colour as valid characters to separate taxa. They did indeed often (but not always) vary independently from each other. However, two vegetative characters were found that consistently separated the C_3 and C_4 forms. These were width of veins in the basal sheath and width of leaf blade 20 mm from the tip (measuring the broadest basal leaf). Fig. 2 shows the scatter diagram produced with these characters on the x- and the y-axis. The two anatomical/physiological forms are separated, on both axes.

It is evident from this diagram that even though short racemes, dark spikelet colour and very hairy leaf blades are often associated with the C_3 form, C_3 plants may occasionally have long racemes, pale spikelet colour and glabrous leaf blades. Conversely, C_4 plants usually have long racemes, pale spikelets and glabrous leaf blades, but they may also have any combination of characters at the other extreme. Intermediate states of these characters can occur in either anatomical form. However, the two forms can always be distinguished by a combination of the

Photo-synthesis	□	C_3
	△	C_4
	○	C-Pathway unknown
Spikelet colour	○	Spikelets pale
	◐	Spikelets medium
	●	Spikelets dark
Raceme length	⤿	Racemes 40 - 60mm
	⤿	Racemes 60 - 80mm
	⤿	Racemes 80 - 100mm
	⤿	Racemes 100 - 120mm
	⤿	Racemes 120 - 140mm
	⤿	Racemes 140 - 160mm
Leaf blade hairiness	∪	Glabrous
	∪	Sparsely hairy
	∪	Moderately hairy
	∪	Densely hairy

FIG. 1. — Character states shown in the scatter diagrams (Figs 2, 3 and 4).

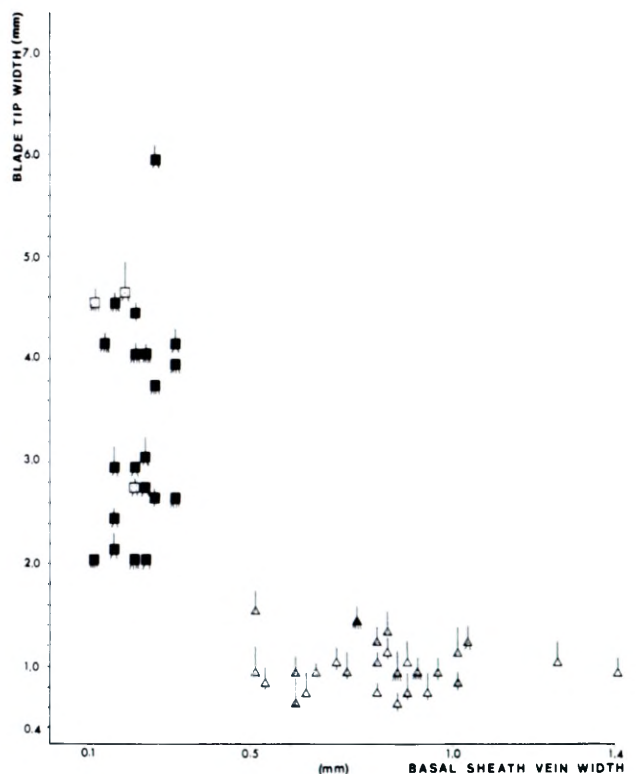


FIG. 2. — Specimens from southern Africa of known C_3 / C_4 state in R.P. Ellis's collection of voucher specimens for anatomical study. (Specimens are listed individually in the systematic treatment of each subspecies.)

width of the veins in the basal sheath and the width of the leaf blade 20 mm from the tip.

Fig. 3 shows a pattern similar to that for Fig. 2 when all the PRE specimens from southern Africa of which the anatomy had not been determined were plotted using the same characters. Again, there is a separation into two groups on the basis of width of veins in the basal sheath and width of the leaf blade near the tip. The similarity of the pattern formed by these specimens, for which the anatomical state is not known, to the pattern formed by Ellis's voucher specimens examined for C_3 or C_4 anatomy, makes it possible to predict the anatomical state. Specimens with narrow veins in the basal sheath and broad leaf tips have C_3 leaf anatomy, and specimens with broad veins in the basal sheath and narrow leaf tips have C_4 anatomy. The characters of short dense dark racemes and markedly hairy leaf blades are often correlated with the C_3 form, and the characters of long loose pale racemes and glabrous leaf blades are often correlated with the C_4 form. However, intermediates and even sometimes the extreme states for these characters can occur in either anatomical form. An interesting sub-group of the C_3 plants with exceptionally broad leaf tips (wider than 4.6 mm) and with a medium-brown spikelet colour, occurs in southern Natal, Transkei and the eastern Cape.

It is worth noting that the specimens of Ellis do not show any C_3 plants with leaf tips narrower than 2.0 mm, but that there are a number with apparently narrower tips among the herbarium specimens plotted. This is probably an artefact of collection. In specimens which are not immediately pressed, the leaf blades roll considerably, and therefore appear

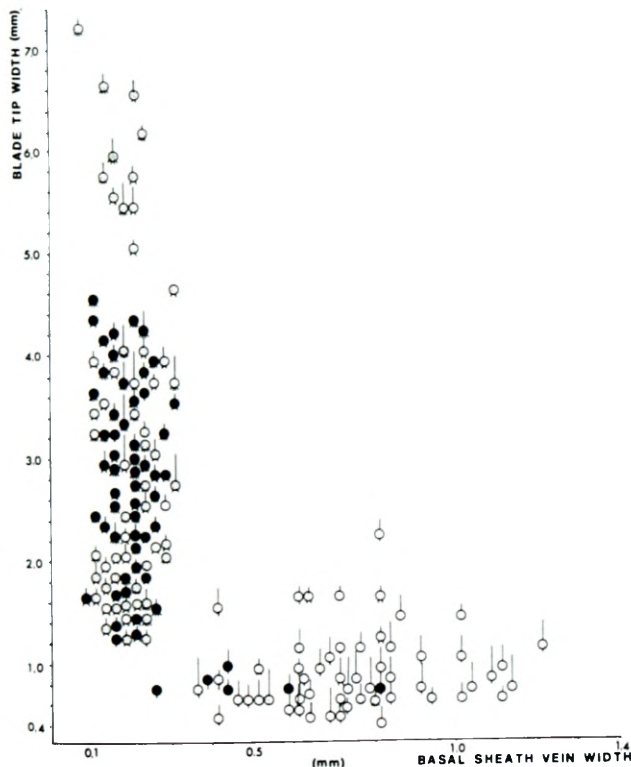


FIG. 3. — Specimens from southern Africa of unknown C_3 / C_4 state, in the herbarium collection at PRE. (Specimens are listed individually in the systematic treatment of each subspecies.)

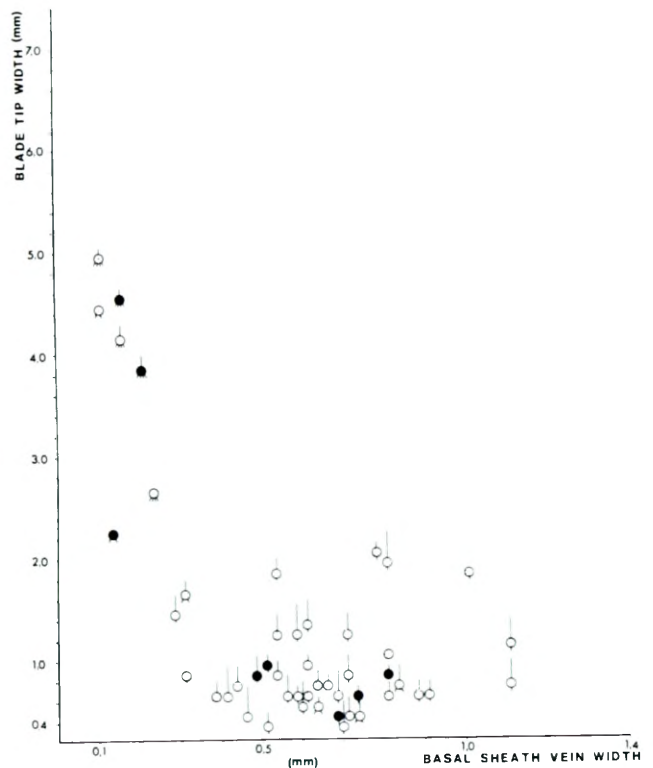


FIG. 4. — Specimens from tropical Africa of unknown C_3 / C_4 state, in the herbarium collection at PRE.

narrower than in the case of Ellis's well-prepared specimens.

Specimens at PRE from tropical Africa that have not been examined anatomically are shown in Fig. 4. Again, there is separation into two groups on the basis of width of veins in the basal sheath and width of leaf blade tip. All the specimens in the C_3 group are from the eastern highlands of Zimbabwe except one from Tanzania collected at an altitude of 1830 m. Ellis (1981) has pointed out that in southern Africa, the C_3 form occupies habitats of higher elevation than the C_4 form. It occurs at the lowest elevations in the Cape and Natal, rising to the central highveld, and in the eastern and northern Transvaal occurring in the Transvaal Drakensberg and in the Soutpansberg. This increase in altitude with decreasing latitude for C_3 plants is therefore borne out by the data from tropical Africa.

MORPHOLOGY

Both the subspecies are robust perennial tufted grasses, with short stout deeply buried rhizomes. The basal portions of the sheath and culms are usually buried to a depth 50–100 mm. The shape in outline of the buried parts is often different in the two subspecies. I subsp. *semialata* (the C_4 form), the lowest portion above the rhizome is often expanded and somewhat bulbous, with the upper section a bit narrower and parallel-sided, whereas in subsp. *eckloniana* (the C_3 form) the lowest portion is not bulbous and the sheaths spread slightly outwards from each other so that the outline is V-shaped. The basal sheaths of both subspecies are usually extremely hairy, with the hairs arising between the veins. The veins of subsp. *semialata* are very wide, and appear as broad yellowish ribs, with the hairs emerging between them. The veins of subsp.

TABLE 1. — Anatomical and physiological features of the subspecies of *A. semialata*

Character	C ₃ form (subsp. <i>eckloniana</i>)	C ₄ form (subsp. <i>semialata</i>)
Leaf blade anatomy (Ellis, 1974a)		
Inner vascular bundle sheath	Mestome sheath of small thickened cells	Parenchyma sheath with inflated cells containing large chloroplasts.
Outer vascular bundle sheath	Parenchyma sheath of large thickened cells with no or few unspecialized chloroplasts.	Thin-walled cells smaller than cells of inner v.b. sheath, with no or few chloroplasts similar to mesophyll chloroplasts.
Chlorenchyma cells	Tabular, indistinctly radiate with larger intercellular air spaces	Larger than v.b. sheath cells, hexagonal to inflated, with small intercellular air spaces.
Leaf surface (Frean <i>et al.</i> , 1980)		
(adaxial surface of leaf 2)		
Area	1 138	674
No. stomata/mm ²	181	70
No. stomata/leaf	206 350	47 180
Ave. area of stomata in 1 mm ²	1,54 × 10 ⁻⁴	3,30 × 10 ⁻⁴
% stomatal area	2,80	2,31
No. epidermal cells/mm ²	1 450	540
Stomatal index	11,2	9,3
Resistance to desiccation (Ellis, 1981)	by concertina pleating	by rolling
Epidermal macrohairs (Frean & Cresswell, 1979)	present	usually absent
Wax crystals	absent	present
Physiology (Frean <i>et al.</i> , (1980)		
(X̄ of plants examined)		
Average photosynthesis (ng / cm ² / s)	21	33
Average transpiration (ug / cm ² / s)	1,60	0,65
Transpiration/photosynthesis ratio	76,5	19,0
Leaf resistance to water loss (Ellis, 1981, reporting B.N. Smith & J. Vogel)	8,5	15,5
Carbon isotope ratios (Ellis, 1981, reporting J. Vogel, unpublished)	-25,2- -28,5	-9,3- -13,8
CO ₂ compensation point	50 ppm	5 ppm
Cytogenetics (Ellis, 1981, reporting W.V. Brown & C. Hsu)		
2n chromosome number	18	18, 36, 54

eckloniana are much narrower and the broad spaces between them are covered with hairs. The hairs in both species are usually so long that the veins are often difficult to see unless some of the hairs are scraped away. A difference between the subspecies that is probably a result of the differences in the veins of the basal sheaths is the tendency of the old sheaths to split into fibres. In subspecies *eckloniana* often the basal sheaths split into fine fibres from the top. In subsp. *semialata* this does not happen, although the thickened veins may sometimes

separate at the base where they curve around to the rhizome.

Leaf blade differences useful in separating the subspecies can sometimes be observed in living plants. Frean *et al.* (1980) report that the leaf blades of the C₃ plants are held erect, and the leaf blades of the C₄ plants droop downwards from the middle. The C₃ plants also usually hold their leaf blades flat, whereas the C₄ plants hold their leaf blades slightly curved upwards at the edges. However, although

these characters can be useful in the field for quick identification, they are not always reliable, especially in places that have been recently burned. Perhaps for this reason, specimens from the Ermelo area are particularly difficult to place in a subspecies on the basis of their leaves. As shown by the scatter diagrams, subsp. *eckloniana* tends to have more hairy leaf blades than subsp. *semialata*, but individuals in each taxon may vary greatly in this respect.

The inflorescence characters of raceme length, density of spikelets on the axes, and spikelet colour are the traditional ones used to separate the two variants but, as has been discussed above, they are not constant and are therefore unreliable.

No spikelet character has been found to separate the subspecies. Subspecies *semialata* tends to have longer spikelets and those of subsp. *eckloniana* tend to be shorter, but there is a great overlap between them in the middle of the range. Other spikelet characteristics, such as nervation and outline, are similar in both subspecies, whereas vesture and degree of winging of the upper glume appear to vary randomly in both subspecies.

ANATOMY AND PHYSIOLOGY

Differences in leaf blade anatomy and physiological differences related to the different photosynthetic pathways for the two subspecies have been reported by a number of authors since the first reports of the unusual condition of *A. semialata* by Ellis (1974a). These reports are summarized in Table 1. The marked differences shown by the C₃ and C₄ forms in a large number of characteristics warrants taxonomic recognition, especially when supported by discernable morphological differences.

DISTRIBUTION AND ECOLOGY

Distribution maps for the two subspecies in southern Africa are given in Figs 5 & 6. Subspecies *eckloniana* extends as far south as the eastern Cape, but *semialata* reaches only to Natal. The ranges of the two taxa overlap for most of the country, but in many of the areas, Ellis (1981) has shown that the C₃ plants grow at higher altitude than the C₄ plants. These patterns agree with the findings of Vogel, Fuls & Ellis (1978), where it is demonstrated that C₃ plants are favoured by higher temperatures. The distribution of both subspecies in South Africa corresponds closely with the area indicated by Vogel *et al.* (1978) as predominantly composed of C₄ grass species (75–95% are C₄).

Ellis (1981) also presents the results of soil analysis which show that in the Transvaal Bankenveld the C₃ form grows on moderately to strongly acid soils, and the C₄ form prefers soils that are only slightly acid. This suggests that the taxa may be kept separate by adaptation to different edaphic conditions, as discussed by Gentry (1980).

In a number of localities near Pretoria, Johannesburg and Middelburg in the Transvaal and Eston and Estcourt in Natal, (Ellis, 1981 and pers. comm.) populations of both sub species grow in close proximity, within 100 metres of each other. Even

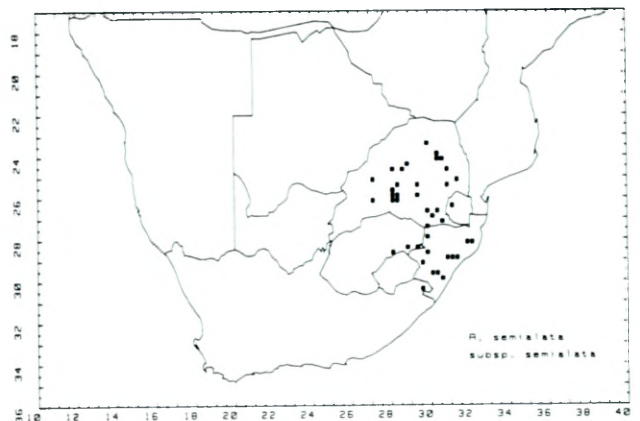


FIG. 5. — Distribution of *Alloteropsis semialata* subsp. *semialata* in southern Africa.

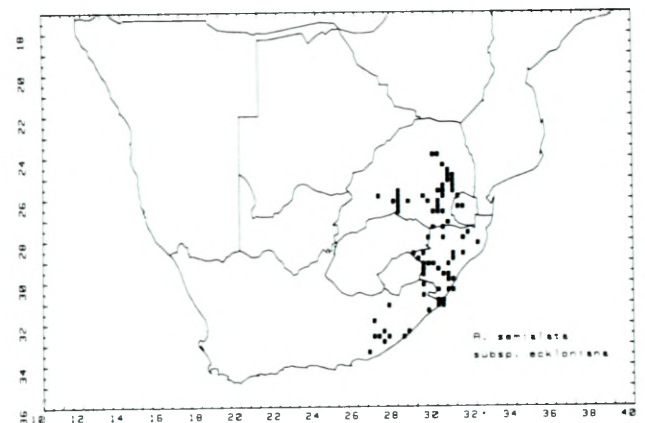


FIG. 6. — Distribution of *Alloteropsis semialata* subsp. *eckloniana* in southern Africa.

here, no intermediates have been found, either in leaf anatomy, C₁₂/C₁₃ ratios, CO₂ compensation point, or in the vegetative characters which indicate the leaf blade anatomy. This indicates that no hybridization has occurred in nature between the two taxa in southern Africa, and is an additional reason for recognizing them as separate entities.

TAXONOMIC TREATMENT

1. *Alloteropsis semialata* (R. Br.) Hitchc. in Contrib. U.S. Nat. Herb. 12: 210 (1909); F.T.A. 9: 483 (1919); Chippind. in Meredith, Grasses & Pastures S. Afr. 423 (1955); Gordon-Gray in Ross, Fl. Natal 80 (1972). Type: Australia, Carpentaria, Brown 6101 (K, iso.!, BM, holo!).

Panicum semialatum R. Br., Prodr. 192 (1810). *Urochloa semialata* (R. Br.) Kunth, Rev. Gram. 1: 31 (1829). *Oplismenus semialatus* (R. Br.) Desv., Opusc. 81 (1831). *Coridochloa semialata* (R. Br.) Nees in Edib. New Phil. 15: 381 (1833). *Axonopus semialatus* (R. Br.) Hook. f. in Fl. Brit. India 7: 64 (1896). *Paspalum semialatum* (R. Br.) Eyles in Trans. Roy. Soc. S. Afr. 5: 299 (1916).

This species is the only known grass with Kranz type leaf anatomy and C₄ carbon metabolism as well as non-Kranz leaf anatomy and C₃ carbon metabolism. These two forms are recognized as subspecies.

Leaf blades rolled or curved upwards, tapering gradually to tip, sparsely hairy, linear, hard-textured; veins on old leaf sheaths at base of culms forming ribs 0.5–1.1 mm across; racemes often (but not always) longer than 80 mm with light coloured spikelets loosely arranged
..... (a) *A. semialata* subsp. *semialata*

Leaf blades flat, tapering abruptly to tip, usually densely hairy; lanceolate, \pm soft-textured; veins on old leaf sheaths at base of culms to 0,3 mm across; racemes often (but not always) shorter than 80 mm with dark coloured spikelets tightly packed together.....

.....(b) *A. semialata* subsp. *eckloniana*

(a) subsp. *semialata*

Tufted perennial with short stout creeping rhizomes; basal parts with old sheaths tightly appressed into a stout bulbous base, parallel sided or ovoid in outline, with very dense hairs to 4 mm long, not splitting into fibres, (rarely splitting from bottom), veins forming broad flat ribs to 0,5–1,1 mm across; culms erect, 300–1300 (–1500) mm tall, nodes woolly, internodes sparsely scabrous to glabrous, base stout, clad in old leaf sheaths. Leaf blades linear, 3–5 (–6) mm wide, usually curved upwards or loosely rolled, tapering gradually to tip, sparsely hairy. Inflorescence of 2–6 digitate racemes 30–220 mm long, sometimes bare near base. Spikelets 5–8 mm long (excluding mucros and awns), tan, brown, or purple, sometimes with dark transverse bars; upper glume abruptly ending in a mucro to 3 mm long, sometimes with marginal flaps; lemmas usually both with awns to 3 mm long. Anatomy of leaf blades is Kranz-type. Carbon metabolism is *C₄*. (Fig. 7.)

Natal and Zululand north through the eastern Orange Free State and Swaziland to the Transvaal; also occurring through eastern, central and west tropical Africa to India, south-east Asia, Malaysia, and northern and eastern Australia. Grows in grasslands, rocky hillsides and bushveld woodland, usually at lower altitudes and in less acid soils than the other subspecies.

TRANSVAAL. — 2330 (Tzaneen): Duiwelskloof (–CA), *Scheepers* 776. Valencia (–CD), *Rinder* 8. 2428 (Nylstroom): Vaalwater (–AB), *Codd* 922. 2430 (Pilgrim's Rest): Mariepskop (–DB), *Van der Schijff* 6152. 2527 (Rustenburg): Pilanesberg (–AA), *Pole Evans* 631; *Smook* 958, 1019. 2528 (Pretoria): Kwandebele (–BD), *Smook* 3160; Pretoria Dist. (–CA), *De Winter* 8645; *Rietondale* (–CA), *Chippindall* 112; Nat. Botanic Garden (–CA), *Crook* 2056; Meintjies Kop (–CA), *Fouche* (PRE) 7648; Elofsdal (–CA), *Hanekom* 1696; Nature Reserve (–CA), *Kok* 237; Pretoria (–CA), *Leendertz* TM 6221; Pretoria Dist. (–CA), *MacDonald* PRE 285; Sunnyside Hill (–CA), *Mogg* 15987; Wonderboom Station (–CA), *Phillips* 3516; Rietfontein (–CA), *Pole Evans* 277; Waterval (–CA), *Pole Evans* 1523; Fountains Valley (–CA), *Skead* 57; Waterkloof (–CA), *Verdoorn* 74; Pretoria (–CA), *Wager* TM 14655; Doornhoogte, Irene (–CC), *Pole Evans* 509; Lyttelton Station (–CC); *Pole Evans* 511; Faerie Glen (–CD), *Group 1* 1; Faerie Glen (–CD), *Group 2* 67; Faerie Glen (–CD), *Group 4* 37. 2529 (Witbank): Loskop Dam Nature Reserve (–AD), *Pettifer* 706; Robbertsloop (–AD), *Theron* 1237; Loskop Dam Nature Reserve (–CB), *Theron* 1. 2530 (Lydenburg): Lowveld Botanical Garden (–BD), *Van Jaarsveld* 168. 3531 (Komatipoort): Pretoriuskop, K.N.P. (–AB), *Van der Schijff* 3374. 2627 (Potchefstroom): Goedgedacht (–AA), *Sutton* 496. 2628 (Johannesburg): Modderfontein (–AA), *Haagner* TM 3781; Benoni (–AB), *Bradfield* 244; Benoni (–AB), *Bradfield* 272; Springs (–AB), *Pretoria* PRE 33955; Klipriviersberg, (–AC), *Cohen* 698; 23 km SE of Greylingstad (–DD), *Acocks* 12556. 2629 (Bethal): Standerton Dist. (–CC), *Burt Davy* 3082; Standerton Dist. (–CD), *Burt Davy* 1020; Ermelo Dist. (–DA), *Burt Davy* 946; Ermelo Dist. (–DA), *Collins* TM 12203, *Collins* TM 13450; Nooitgedacht (–DB), *Henrici* 1201; Nooitgedacht (–DB), *Henrici* 1206; Nooitgedacht (–DB), *Henrici* 1285; Ermelo Dist. (–DB), *Tennant* PRE 289. 2630 (Carolina): Athole Pasture Research Station (–CB), *Norval* 83; Athole Pasture Research Station (–CB), *Norval* 119.



FIG. 7. — Habit of *Alloteropsis semialata* subsp. *semialata*.

SWAZILAND. — 2631 (Mbabane): Mlilwane Wildlife Sanctuary (–AC), *Stephen* 1421; Tshaneni (–BB), *Barrett* 209.

NATAL. — (Harrismith): Slopes of Dooley (–CC), *Doidge* PRE 33928. 2830 (Dundee): Kranskop (–DD), *Stirton* 5224. 2831 (Nkandla): Corridor between Hluhluwe and Umfolozi (–BB), *Hitchins* 665; Corridor between Hluhluwe and Umfolozi (–BB), *Hitchins* 716; Umhlatuzi Lake (–CC), *Venter* 3872; Hluhluwe

Game Reserve (-CD), *Bourquin 640*; Eshowe (-CD), *Halse 59*. 3832 (Mtubatuba): Hluhluwe Game Reserve (-AA), *Hitchins 537*. 2929 (Underberg): Ntabamhlope (-BA), *Miller 349*. 2930 (Pietermaritzburg): Oribi (-CA), *Lawson 591*; Pietermaritzburg (-CB), *Goossens 152*.

C₄ Vouchers

TRANSVAAL. — 2329 (Pietersburg): 13 km from Bandolierkop (-BD), *Ellis 3482*; 17 km from Soekmekaar (-BD), *Ellis 3483, 3484*. 2330 (Tzaneen): 15 km from Tzaneen (-CD), *Ellis 3486*. 2428 (Nylstroom): Doorndraai Dam Nature Reserve (-BD), *Ellis 3497*; Kranskop, Nylstroom Dist. (-CA), *Ellis 3506*; 5 km from Naboomspruit (-DA), *Ellis 3815*. 2430 (Pilgrim's Rest): 2 km from Ofcolaco (-AB), *Ellis 2809*; 35 km from Tzaneen (-BA), *Ellis 3813*. 2528 (Pretoria): Nasionale Botaniese Tuin (-CA), *Manders 9*. 2529 (Witbank): 3 km north of Middelburg (-CD), *Ellis 2832, 2833*; 2 km from Middelburg (-CD), *Ellis 3810*. 2629 (Bethal): 8 km from Ermelo (-DB), *Ellis 3527, 3528, 3807*; 28 km from Ermelo (-DB), *Ellis 3808*. 2630 (Carolina): 35 km from Ermelo (-CC), *Ellis 3530*. 2730 (Vryheid): Kwamandlangampisi Mts (-BA), *Ellis 3532, 3534*.

O.F.S. — 2727 (Kroonstad): Heilbron (-BD), *Brandmuller 47*. 2828 (Bethlehem): Witsieshoek Dist. (-BD), *Ellis 1938*.

NATAL. — 2729 (Volksrust): Majuba Pass (-BD), *Ellis 3769*; 25 km from Newcastle (-DD), *Ellis 3770*. 2829 (Harrismith): Van Reenen's Pass (-AD), *Ellis 3805*; 17 km from Ladysmith (-DB), *Ellis 3771*. 3832 (Mtubatuba): 19 km south of Mtubatuba (-AC), *Strey 5615*. 2930 (Pietermaritzburg): Eston (-DC), *Ellis 3775*.

(b) *subsp. eckloniana* (Nees) Gibbs Russell, stat. nov.

Bluffia eckloniana Nees in *Lehm., Ind. Sem. Hort. Hamb.* 1834 8 (1834), *Fl. Afr. Austr.* 61 (1841). *Panicum semialatum* R. Br. var. *ecklonianum* (Nees) Dur. & Schinz, *Consp. Fl. Afr.* 5: 764 (1894). *Axonopus semialatus* (R. Br.) Hook f. var. *ecklonii* Stapf in *Fl. Cap.* 7: 418 (1899), nom. superfl., based on *Bluffia eckloniana* Nees. *Axonopus ecklonianus* (Nees) Chiov. in *Ann. Bot. Roma* 13: 47 (1914). *Alloteropsis eckloniana* (Nees) Hitchc. in *Proc. Biol. Soc. Wash.* 29: 128 (1916). *Paspalum semialatum* (R. Br.) Eyles var. *ecklonii* (Stapf) Eyles in *Trans. Roy. Soc. S. Afr.* 5: 299 (1916), nom. superfl. *Alloteropsis semialata* (R. Br.) Hitchc. var. *ecklonii* (Stapf) Stapf in *F.T.A.* 9: 485 (1919), nom. superfl. *Axonopus semialatus* (R. Br.) Hook. f. var. *ecklonianus* (Nees) Peter in *F.D.O. -A.* 1: 165 (1929). *Alloteropsis semialata* (R. Br.) Hitchc. var. *eckloniana* (Nees) C.E. Hubb. in *Bor. Grasses Burma, Ceylon, India, Pakistan* 277 (1960). Isotypes: Katberg, *Drège* (S; K!, isosyn; fragment in PRE!), Port Natal, *Drège* (S, isosyn.).

Similar to the typical subspecies in spikelet structure, but differing in vegetative morphology and often in inflorescence size and colour. *Basal parts* with sheaths usually somewhat separated, base V-shaped in outline, not bulbous, with dense hairs less than 3 mm long, often splitting into fibres from top or middle, veins to 0.3 mm across. *Culms* 250–1100 mm tall, nodes woolly to velutinous, internodes velutinous to glabrous. *Leaf blades* linear-lanceolate, flat, 3–12 mm wide, tapering abruptly to tip, velutinous (rarely only sparsely hairy). *Inflorescence* of 3–7 (–9) racemes 25–90 (–120) mm long, frequently with 1 or 2 racemes branching lower than others which are digitate. *Spikelets* usually dark brown or purplish black, sometimes lighter or barred. *Anatomy* of leaf blades is non-Krantz type. *Carbon metabolism* is C₃. (Fig. 8.)

Eastern Cape northward through Natal to the eastern Orange Free State and the Transvaal; occurring as far north at the eastern highlands of Zimbabwe and mountainous regions of Tanzania. Grows in grassland, on mountain and hillsides often

in rocky places, and on forest margins, usually at higher altitudes and in more acid soils than the typical subspecies.

TRANSVAAL. — 2329 (Pietersburg): Haenertsburg (-DD), *Acocks & Hafstrom 60*; Magoebaskloof, (-DD), *Crawford 286*; Haenertsburg (-DD), *Davidse & Loxton 5813*; Iron Crown Mt



FIG. 8. — Habit of *Alloteropsis semialata* subsp. *eckloniana*.

(-DD), *Mogg 16640*. 2330 (Tzaneen); Grootbosch Forest Reserve, Duiwelskloof (-CA), *Scheepers 835*; New Agatha Forest (-CC), *Muller & Scheepers 217*; Woodbush (-CC), *Wager TM 12518*. 2430 (Pilgrim's Rest); Ohrigstad Nature Reserve (-DA), *Jacobsen 1293*; Dam (-DC), *Jacobsen 2271*; Mac Mac Nature Reserve (-DD), *Kluge 1926*. 2527 (Rustenburg); Derby Station (-CC), *Burt Davy 7170*; 2528 (Pretoria); Waterkloof (-CA), *Mogg 15049*; Groenkloof (-CC), *Pentz PRE 33973*. 2530 (Lydenburg); Schoemanskloof (-AD), *Smuts 261*; Long Tom Pass (-BA), *Du Toit 1037*; Klipbankspruit (-BA), *Du Toit 1047*; Hartebeestvlakte (-BA), *Mohle 30*; Mauchberg (-BB), *Smuts & Gillett 2300*; Witklop (-BD), *Kluge 204*; Belfast (-CA), *Jenkins TM 6876*; Belfast (-CA), *Leendertz 2699*; Machadodorp (-CB), *Galpin 13104*; Skoonwater Farm (-CD), *Smook 894*; Nelshoogte (-DB), *Muller 2125*; Devils Kantoort, Kaapsehoop (-DB), *Pole Evans 1006*. 2531 (Komatipoort); Twello Forest (-CC), *Buitendag 699*; Schagen (-CC), *Liebenberg 2400*; Barberton (-CC), *Pott-Leendertz 5522*; Barberton (-CC), *Pott-Leendertz 5523*; Barberton Dist. (-CC), *Rogers 30270*. 2628 (Johannesburg); Turfontein (-AA), *Bryant D3*; Houghton Estate, (-AA), *Bryant C49*; Crescent Creek (-AA), *Cook 875*; Germiston (-AA), *Fenn PRE 316*; Johannesburg (-AA), *Leendertz TM 6058*; Kelland (-AA), *Liebenberg 8413*; Elsberg (-AA), *Rogers 12132*; Klipriviersberg (-AC), *Marloth 3858*; Suikerbosrand Nature Reserve (-CA), *Bredenkamp 853*. 2629 (Bethal); Ermelo Dist. (-DB), *Kuhne PRE 33937*. 2630 (Carolina); Carolina Dist. (-AA), *Burt Davy 7367*; Leeuwoort (-AA), *Burt Davy 7446*; Chrissiemer (-AC), *Theron 2408*; Coalbank Siding (-AD), *Malcolm PRE 7806*; Mavriestad East (-CA), *Pott-Leendertz 5214* Athole Pasture Research Station (-CB), *Norval 57*.

O.F.S. — 2729 (Volksrust); Mont Pelaa (-DC), *Ferreira FO38*.

SWAZILAND.— 2631 (Mbabane); Mbabane (-AC), *Burt Davy 2872*; Dalriach (-AC), *Compton 27158*; 16 km E of Mbabane (-AD), *Edwards 309*.

NATAL — (Vryheid); Wakkerstroom (-AD), *Smook 1202*; Vryheid Dist. (-CD), *Burt Davy 11424*. 2731 (Louwsburg); Ngomi Forest (-CD), *Gerstner 4476*; Lower Mkuze Valley (-DA), *Ward 7269*. 2828 (Bethlehem); Royal Nat'ar National Park (-DB), *Galpin 10353*. 2829 (Harrismith); Acton Homes (-CB), *Doidge 33939*; Mnweni, Drakensberg (-CC), *Estterhuysen 18675*. 2830 (Dundee); Ouden, Ntschiza (-DB), *Edwards 2228*; Kranskop (-DD), *Stirton 5208*. 2831 (Nkandla); Umfulazane, Melmouth Dist. (-DB), *Mogg 4567*. 2832 (Mtubatuba); Hluhluwe Game Reserve (-AA), *Hitchins 106*. 2929 (Underberg); Cathkin Peak (-AB), *Gluckman 24963*; Giant's Castle (-AB), *Nicholson 2*; Giant's Castle (-AB), *Trauseld 845*; Tabamhlope Reserve (-BA), *West 458*; Drakensberg (-CB), *Werderman 1415*. 2930 (Pietermaritzburg); Shafton, Howick (-AC), *Hutton TM 2672*; Ligetton (-AC), *Mogg 1406*; Caversham (-AC), *Mogg 2402*; Tweedie (-AC), *Mogg 3467*; Balgowan, Glen Arum (-AC), *Mogg 5599*; Balgowan (-AC), *Stirton 5411*; Greytown (-BA), *Stirton 5086*; Zwartkop Location, Lions River (-CB), *Moll 1117*; Cedara Agricultural College (-CB), *Phillips 3452*; Drummond (-DA), *Galpin 10284*; Key Ridge, Drummond (-DC), *Stirton 5558*; Kloof, Pinetown Dist. (-DD), *Galpin 12260*; Claremont (-DD), *Medley-Wood 7648*; Gillits, Pinetown Dist. (-DD), *Moll 1922*. 3029 (Kokstad); Bushman's Nek (-AB), *Smook 1702*. 3030 (Port Shepstone); Mgaye (-BC), *Rudatis 733*; Mgayi (-BC), *Ward 6333*; Scottburgh (-BD), *Goossens 1703*; Murchison Flats (-CC), *Maclean 322*; Port Shepstone (-CD), *Henrici PRE 33943*. 3130 (Port Edward); Port Edward (-AA), *Ward 6667*; Port Edward (-AB), *Du Toit 912*; Port Edward (-AB), *Du Toit 942*.

CAPE. — (Kokstad); Kokstad (-CB), *Coleman 924*. 3126 (Queenstown); Hangklip Mt. (-DD), *Galpin 5858*. 3127 (Lady Frere) Kopshorn (-BA), *Viljoen 193*. 3129 (Port St. Johns); Ntsubane (-BC), *Strey 9001*. 3227 (Stutterheim); Fort Cunynghame (-AD), *Sim 2792*; Ghulu Kop, Amatola Mts (-CA), *Dyer 255*; Nyameni Forest (-CA), *Dyer 256*; Gxulu Kop (-CA), *Gibbs Russell 3447*; Dohne Experiment Station (-CB), *Botha 9*; Evelyn Valley Forest (-CD), *Von Broembsen 116*; Kei Road Station (-DA), *Ranger 8*. 3228 (Butterworth); Kentani Dist. (-BC), *Pegler 70*; Kei Mouth (-CB), *Flanagan 928*. 3325 (Port Elizabeth); Atalaya Valley, Zuurberg (-BC), *Archibald 5283*. 3326 (Grahamstown); Grahamstown (-BC), *Britten 6492*; 8 miles from Grahamstown (-BC), *Comins 1014*; Grahamstown Dist.

(-BC), *Godfrey SH1341*; On mountain, Grahamstown Dist. (-BC), *Zeyher 4466*.

C₃ Vouchers

TRANSVAAL — 2329 (Pietersburg); Top of Magoebaskloof Pass (-DD), *Ellis 3814*. 2430 (Pilgrim's Rest); Drakensberg Mts, NE of Penge (-AD), *Ellis 2812, 2813, 2830*. 2529 (Witbank); 5 km from Middelburg (-CD), *Ellis 2836*; 2 km from Middelburg (-CD), *Ellis 3811*. 2530 (Lydenburg); 5 km from Machadodorp (-CB), *Ellis 3812*. 2628 (Johannesburg); Delmas (-BA), *Ellis 3806*. 2629 (Bethal) 32 km from Middelburg (-BA), *Ellis 3809*. 2730 (Vryheid); Kwamandlangampisi Mts (-BA), *Ellis 3533*.

NATAL — 2729 (Volksrust); Majuba Pass (-BD), *Ellis 3768*. 2731 (Louwsburg); 16 km from Ngome Forest (-CD), *Ellis 3348*. 2929 (Underberg); Cathedral Peak Forest Reserve (-AD), *Ellis 3271*; 21 km from Estcourt (-BB), *Ellis 3773*. 2930 (Pietermaritzburg); 8 km from Balgowan (-AC), *Ellis 3774*. 3030 (Port Shepstone); 7 km from Highflats (-AC), *Ellis 3804*; Trafalgar Beach (-CD), *Ellis 3779*; Izotsha Station (-CD), *Ellis 3797*.

CONCLUSION

The variation within *Alloteropsis semialata* in leaf blade anatomy and photosynthetic pathway is recognized at the level of subspecies. This rank is chosen because, although the taxa are separate in southern Africa, their behaviour throughout their entire range is not known. Intermediate photosynthetic types occur in tropical Africa. Ellis (1981) reports that *Milne-Redhead 3021* from Mwinilunga District, Zambia, has an intermediate carbon isotope ratio of -20,0 and is the only known example of a grass with this intermediate state. Three specimens from tropical Africa appear to be intermediate in the morphological characters that indicate the photosynthetic pathway as shown in Fig. 4. These are *Eyles 1920* from Harare, Zimbabwe, *Greenway 6290* from Chinjanje Valley, Malawi, and *Milne-Redhead 3371* from Mwinilunga District, Zambia.

These intermediate forms merit closer study, especially because a species with anatomical characteristics intermediate between C₃ and C₄, *Neurachne lanigera* S.T Blake, has been reported from Australia (Hattersley *et al.*, 1982). This indicates that the situation in *Alloteropsis* may not be unique, and that within the Paniceae the understanding of the differences in photosynthetic pathways may lead to a clearer understanding of their evolution.

The taxonomic evaluation of anatomical and physiological data and its correlation with morphological characters presented in this paper has been possible only because voucher herbarium specimens prepared by Ellis and his co-workers were available. It is an outstanding example of the fact that taxonomy can fulfil its synthesizing role of evaluating as many characters as possible only when work done in other botanical disciplines is permanently recorded by voucher specimens. The voucher specimens establish the link between the morphological characters visible on the specimens, the distribution data recorded on the label, and the results of experimental or anatomical investigations.

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UITTREKSEL

Alloteropsis semialata (R. Br.) Hitchc. sensu Chippindall (1955) en Clayton (in druk) is die enigste bekende grasspesie met beide Kranz en nie-Kranz blaaranatomie en dus met beide die C₃ en C₄ fotosinteseoetes. In die verlede is twee taksons erken maar die kenmerke wat gebruik is om hulle te skei, is as onbetroubaar bewys. Gevolglik is hulle verenig. Die sorgvuldige bestudering van kontrole herbariumeksemplare vir anatomiese en fisiologiese werk het egter getoon dat C₃ en C₄ taksons geskei kan word op grond van morfologiese kenmerke wat verskil van dié wat in die verlede gebruik is. Twee taksons word gevolglik weer erken op die subspesievlak en die naam *Alloteropsis semialata* subsp. **eckloniana** (Nees) Gibbs Russell stat. nov. word gepubliseer.

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