PART 1

THE TAXONOMY OF THE SUBTRIBE *AVENINAE* EXCLUDING *HELICTOTRICHON* SCHULT.

PART 2

I. THE VARIATION PATTERNS IN *FESTUCA CAPRINA* NEES

II. A NEW SPECIES IN THE GENUS *FESTUCA* L.

BY

TAMSANQA MTHUNZI SOKUTU

DISSERTATION

Submitted in partial fulfilment of the

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Master of Science

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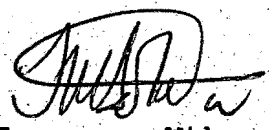
I declare that this dissertation is my own work, and that all the sources I have used or quoted have been indicated and acknwoledged by means of complete references. No part of this dissertation has been submitted for examination in any other university.



Tamsanqa Mthunzi Sokutu

PART 1

THE TAXONOMY OF THE SUBTRIBE AVENINAE EXCLUDING *HELICTOTRICHON* SCHULT.

TABLE OF CONTENTS

ABSTRACT

The sub-tribe *Aveninae* Presl in southern Africa is represented by nine genera, eight of which are included in this study. Most of these genera have been introduced from elsewhere, in most cases from Europe. A morphological and anatomical account of this subtribe excluding *Helictotrichon* Schult. is given and keys to genera and species are also provided. Characters that are employed in Flora Europaea to differentiate between genera and species have, with few exceptions, been found to be useful.

ACKNOWLEDGEMENTS

This study was done while holding an FRD studentship. I am grateful to my project adviser Dr. H.P. Linder for his assistance during this project, staff members in the Systematics Laboratory and other members of the Botany Department, University of Cape Town, who helped at one time or another during this study. I also thank Prof. A.V. Hall of the University of Cape Town who was responsible for supervising the final draft of this thesis.

The photographic expertise of Miss. M. Koekemoer and Mrs. A. Romanowski of National Botanic Institute is gratefully acknowledged.

Finally, I dedicate this thesis to my mother, my family and my wife, Nosisi, whose support and encouragement was invaluable during the period of this study.

INTRODUCTION

Aveneae Dumort is a tribe of grasses of the subfamily Pooideae with about 57 genera mostly from temperate and cold regions (Chippindall, 1955; Clayton, 1970; Clayton and Renvoize, 1986). This study will concentrate on the sub-tribe *Aveninae* Presl. The taxonomy of the sub-tribe *Aveninae* as represented in Southern Africa is not clearly understood. Most of the members of this group in the Flora of Southern African (F.S.A.) region were introduced from elsewhere. Therefore they only form a subset of the world's *Avenineae* and the concepts by which they are presented here can only be viewed in that context.

Apart from a contribution by Chippindall (1955) no work has been done on the taxonomy of these introduced grasses in the Flora of Southern Africa (F.S.A.) region.

The study of the introduced grasses is important in that it will shed some light on how they affect the indigenous taxa. A study of this nature can also give insight to the biology of the species concerned, their ecological preferences, subsistence biology, etc. Such an understanding may be important for the control or exploitation of such grasses and can also act as a foundation for more detailed biosystematic analyses. Such analyses cannot be conducted without a proper taxonomical knowledge of the plants.

The aim of this work therefore is to produce an extensive descriptive account of the morphology, and anatomy and taxonomy of the species in this sub-tribe as found in the F.S.A. region. A

brief account of the ecological preferences of each species will be given. Comparisons will only be made in cases where clarity is lacking between the taxa concerned.

In the F.S.A. region members of the Aveninae occur chiefly in mountain grasslands, forests and wet places; and the genus *Avena* is common in disturbed areas (Chippindall, 1955). Of the ten genera that occur in F.S.A. region, eight have been introduced although some of them may be naturalised. These include *Holcus* L., *Koeleria* Pers., *Periballia* Trin., *Arrhenatherum* Beav., *Avena* L., *Lophochloa* Reichenb., *Deschampsia* Beauv., and *Aira* L.. *Holcus* L. includes one indigenous species. *Helictotrichon* Schult. is not included in this study due to its large number of species and its taxonomical complexity. Following a number of discussions with prominent taxonomists including G.E. Gibbs-Russell in this region it was decided that although Clayton and Renvoize (1986) are using *Rostraria* for *Lophochloa*, the latter should be used for this region as there is still a lack of clarity about this matter. Gibbs Russell et al. (1989) have consequently used *Lophochloa* as well.

In this study infra-specific taxa have not been formally recognised. This is a result of a lack of enough material for comparison purposes and the complexity of variation at this level.

The results obtained in this study confirm that most of the genera and species in the *Aveninae* are weeds in South Africa although some have become naturalised. Most of these species can

be easily distinguished from each other, except for some species in *Avena* and *Aira*. The species within these genera are not always easy to distinguish from each other. This is due to the variability of characters upon which these species are delimited.

All the genera studied here can be easily recognised in the Flora of Southern African region.

MATERIALS AND METHODS

Morphology

This study is based mainly on herbarium material. Very few collections of *Avena*, *Koeleria* and *Aira* were made by myself. Specimens studied are housed at BOL, PRE, SAM, STE, and NBG. Examination of structures and measurements were made under a dissection microscope at variable magnifications depending on the size of the structure studied. Lodicules were studied after reconstitution in soapy boiling water.

Although all the available specimens were studied, measurements were only taken from 15 - 20 specimens where more than 20 specimens were available. Data on specimen sheets were recorded. Ecological data and phenological data were also recorded mainly from the specimen sheets and from literature. Distribution data were compiled from the literature.

Leaf Anatomy

Pieces of leaves about 3 cm long were soaked in different media to determine the medium that produced the best reconstituted leaves. The treatments were as follows: i) four days in concentrated ammonia ii) in boiling water for approximately one minute; iii) in 70% alcohol at 60 degrees C over night. After the trial run it was evident that the concentrated ammonia gave the best results.

Pieces of leaves about 3 cm long from all the species under study were then soaked in concentrated ammonia for four days. After rinsing in water they were fixed in F.A.A. for 24 hrs, then desilicified in 80% Hydroflouric acid for twelve hours. After rinsing in water for about one hour they were subjected to a dehydration process in a Sakura tissue processor (Fisher scientific) as follows: two changes of eight hours each in:

i) 70% alcohol
ii) 100% alcohol
iii) n-Propanol
iv) n-butanol.

After dehydration the pieces of leaves were embedded by soaking in two changes of melted pure wax (Paraplast+) for twenty-four hours each. Cross sections about 15-20 microns thick were obtained using a rotary microtome. The leaf cross sections were double stained by using Safranin and Fast Green. They were then mounted permanently in DPX (Feder & O'Brien, 1968). Camera lucida drawings were made from the cross sections.

This method had a low success rate in reconstituting the dried leaves. Some leaf cross sections remained partly flattened. Although it is possible that the specimens required to be left longer in the reconstitution medium, I suggest that more investigation should be made on the possibility of fully reconstituting dried specimens. The terminology used in the anatomical descriptions follows Ellis (1976).

DESCRIPTIONS

AVENINAE Presl, Rel. Haenk. 1: 246 (1830). *Airinae* Fries, Summa veg. Scand. 1: 77 (1846). *Holcinae* Dumort. in Bull. Soc. Bot. Belg. 7: 68 (1868). *Graphephorinae* Asch. & Graeb., Syn. Mitteleur. Fl. 2, 1: 342 (1900). *Koeleriinae* Ash. & Graeb l.c. *Airopsidinae* Rouy, Fl. France 14: 99 (1913). *Corynephorinae* Jirasek & Chrtek in Preslia 34: 381 (1962). *Aristaveninae* Albders & Butzin in Willdenowia 8: 82 (1977).

Plants annual or perennial, solitary, several stemmed to densely caespitose. Ligule membranous. Inflorescence a panicle. Spikelets with 2 to several fertile florets, laterally compressed. Glumes equal or unequal, membranous, commonly nitid with hyaline margins; lemmas membranous to coriaceous, typically dorsally awned, awn often geniculate with twisted column. Lodicules 2, commonly fleshy at base. Stigmas 2. Caryopsis commonly ellipsoid; endosperm occasionally soft or liquid.

There are nine genera in this sub-tribe in the F.S.A. region. This study includes eight of them; viz: *Avena* L., *Arrhenatherum*

Beauv., *Holcus* L., *Lophochloa* Reichenb., *Deschampsia* Beauv., *Koeleria* Pers., *Periballia* Trin. and *Aira* L..

Key to genera

1. Spikelets 16mm - 46mm long 4.*Avena*
1. Spikelets less than 16mm long.....2

2. Spikeletes 2 flowered; lower floret male with geniculate awn 6.*Arrhenatherum*
2. Spikelets 2-6 flowered; lower floret bisexual..3

3. Panicle spiciform; pedicels obscured by spikelets; palea gaping 7.*Koeleria*
3. Panicle open or contracted; pedicels not obscured by spikelets; palea not gaping 4

4. Upper lemma with hooked awn; florets falling entire; lower floret bisexual; upper male or sterile 3.*Holcus*
4. Upper lemma without hooked awn; rest of spikelets not as above 5

5. Spikelets 3 - 6 flowered.....2.*Lophochloa*
5. Spikelets 2 flowered.....6

6. Lemmas awnless 8.*Periballia*
6. Lemmas awned.....7

7. Plants annual; lemma apices minutely bifid.....5.*Aira*
7. Plants perennial; lemma apices shortly toothed or notched 1.*Deschampsia*

1. *Deschampsia* Beauv., Ess. Agrost.: 91 (1812); Chippindall, Grasses and Pastures of South Africa: 85 (1955); Clayton, F.T.E.A.: 91 (1970); Dyer, The Genera of southern African Flowering Plants 2: 833 (1976); Clarke, Fl. Europ. 5: 225 (1980); Clayton and Renvoize, Genera Graminum: 129 (1986).

Aira L. Sp. Pl.: 64 (1753) p.p.

Plants perennial, caespitose, sometimes rhizomatous. **Leaves** sometimes basal; convolute or expanded; ligule membranous, sub-acute or deeply lobed, glabrous. **Inflorescence** open, sometimes contracted, ovate to oblong. **Pedicels** erect, not obscured by spikelets. **Spikelets** numerous, narrowly oblong or ovate, 2-flowered. **Glumes** subequal, slightly shorter or longer than the lemmas, lower lanceolate or elliptic, acute, 1 - nerved, upper ovate to lanceolate, 3 - nerved. **Callus** minutely to densely bearded. **Rachilla** internode glabrous or pubescent, lower one missing. **Lemmas** shortly toothed or emarginate, awned. **Awn** almost basal. **Lodicules** fleshy at base. **Anthers** brown.

A genus of about 40 species in temperate and cold regions of the world (Clayton and Renvoize, 1986). It is represented in southern Africa by only two naturalised species. This genus is close to *Aira* from which it may be distinguished by a combination of characters such as its perennial, tussocky habit and the polished cartilaginous or hyaline lemmas with 4 toothed or emarginate apices. Some of the differences between the species of this genus are represented in Fig.1.

Leaves convolute, setaceous; awn geniculate, well exserted beyond

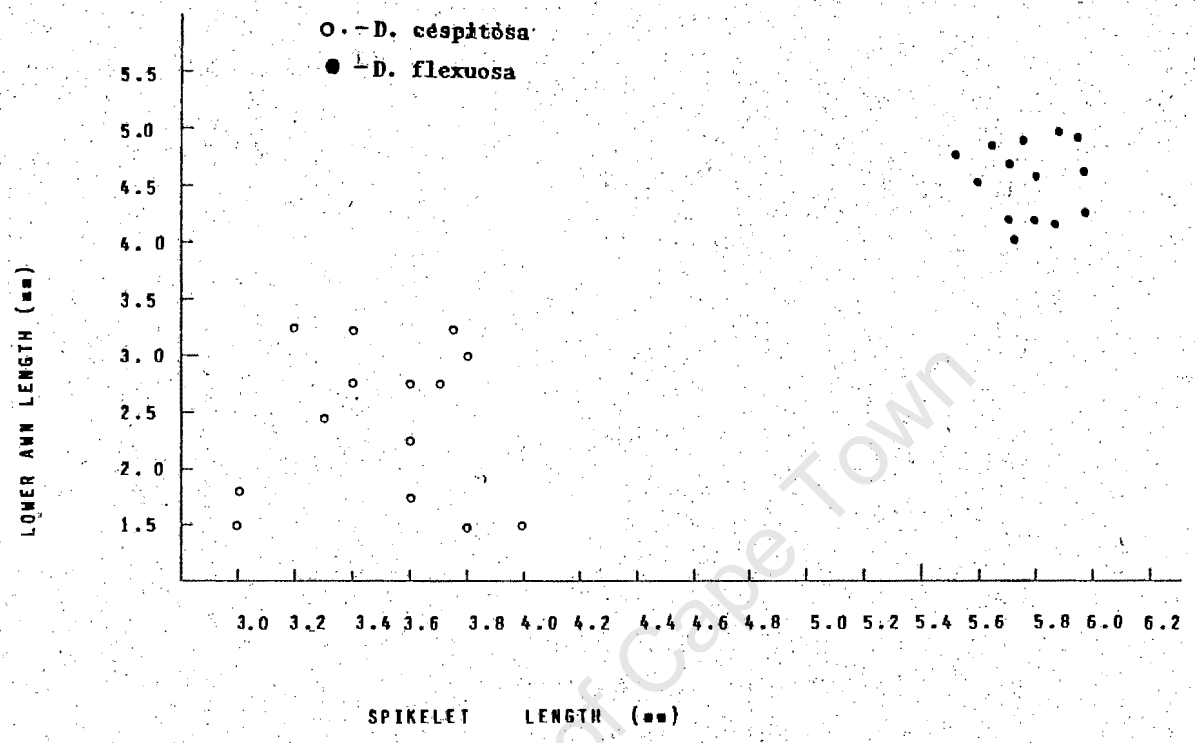


Fig. 1. Scatter diagram showing variation in Descahmpsia, with D. cespitosa and D. flexuosa.

glumes; lemma apices notched .....2.*D. flexuosa*

Leaves expanded, sometimes inrolled; awn almost straight, hardly exserted beyond glumes; lemma apices emarginate

.....1.*D. cespitosa*

1. *Deschampsia cespitosa* (L.) Beauv., Ess. Agrost.: 91 (1812); Phillips, Flora Leribe: 361 (1911); S.A. Grasses: 92 (1931); Hubbard, Grasses: 227 (1954); Chippindall, Grasses and Pastures of South Africa: 85 (1955); Clayton, F.T.E.A.: 92 (1970); Jacot-Guillarmod, Fl. Lesotho: 112 (1971); Clarke, Fl. Europ. 5:225 (1980).

Aira cespitosa L., Sp. Pl: 64 (1753); Type: s.l. (holo. LINN-Microfiche, BOL.!).

Note: The microfiche image of this specimen is not very clear but the general gross morphological appearance seem to agree with the description of *D. cespitosa*.

Plants perennial, caespitose to densely so, sometimes rhizome wanting. **Culms** slender to slightly robust, erect, 25 -- 85cm tall, simple with approximately 2 - 3 nodes; surface smooth, nitid; apical internode exserted from upper sheath. **Leaves** sometimes basal; sheaths loosely rolled on culms, glabrous; leaf blades expanded or convolute, 7 -- 19,5cm long, 2 -- 4mm wide, scabrid on both surfaces, acute, pungent; margin scabrid; ligule membranous, sub-acute, glabrous, 5 -- 11.5mm long. **Inflorescence** oblong to ovate, loose, sometimes contracted, 12 -- 25cm long, nodes 8 -12, rachis glabrous to scaberulous; branches slender,

almost filiform, in alternate clusters along the rachis. **Pedicels** erect, not obscured by the spikelets, scabrid; apex gradually thickened. **Spikelets** numerous, narrowly oblong, 2- flowered, green sometimes purple, 3 -- 4mm long, clustered towards branch tips. **Glumes** subequal, lower glume lanceolate to elliptic, 1-nerved, upper ovate to lanceolate, 3-nerved, acute, glabrous, sometimes scaberulous, more so along the keels, nitid, 2.5 -- 3.5mm long; slightly shorter than the lemmas. **Callus** densely bearded. **Rachilla** glabrous, lower one up to 0.5mm long, upper up to three times as long. **Lemma** ovate or oblong, glabrous, 3 - 4mm long, as long as the glumes, emarginate, notched at apex, awned. **Awn** straight or slightly bent, 1.5 -- 3.5mm long, almost basal, slightly exceeding the lemmas. **Lodicule** fleshy at base, 0.6 -- 0.7mm long. **Palea** two-keeled, almost equal to lemmas. **Anthers** brown, 1.4 -- 1.7mm long.

Leaf Anatomy

Leaf outline: slightly acicular to u-shaped, keel not well developed. **Adaxial ribs and furrows:** present between all vascular bundles, ribs 7, slightly wide, furrows deep, narrow. No abaxial ribs and furrows. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** follows a basic pattern, first order vascular bundles alternate with second order vascular bundles, towards the margins first order vascular bundles are replaced by second order vascular bundles, the latter replaced by third order vascular bundles. Vascular bundles 6-7, round to oval, corresponding to the ribs, situated in the centre of the blade. Phloem distinct

from xylem, not lignified, adjoins the inner vascular bundle sheath. Metaxylem cells conspicuous, in groups of 4 or 5. **Vascular bundle sheath:** double, outer bundle sheath composed of more or less isodiameteric parenchyma cells, abaxial side not covered by the outer bundle sheath, cells smaller than the mesophyll cells, lacking chloroplasts. Mestome sheath cells smaller than the outer bundle sheath cells, sometimes radially thickened. **Sclerenchyma:** abaxial and adaxial sclerenchyma strands always present. Abaxial sclerenchyma forms an interrupted band opposite each vascular bundle, adjacent to the epidermal cells. **Parenchyma girders:** lacking. **Mesophyll:** irregular; tending to radiate, cell shape irregular, intercellular spaces infrequent. Lateral cell count more than 4, continuous between bundles. **Adaxial epidermis:** cells smaller than abaxial epidermal cells. Bulliform cells distinct, large, in groups of three at base of furrow, stomata present. Prickles present. **Abaxial epidermis:** stomata lacking, cells bigger than adaxial epidermal cells. Cuticle present, forms a thin layer. Anatomy festucoid.

Flowering time: January - March

Distribution, Ecology and Delimitation of species:

Deschampsia cespitosa is of European origin, naturalised in the F.S.A. region in Lesotho and the Cape (Fig. 2). It is found in typical grassland habitats in Lesotho and interspersed with fynbos vegetation in the Cape, usually in damp, relatively nutrient rich soil at high altitudes.

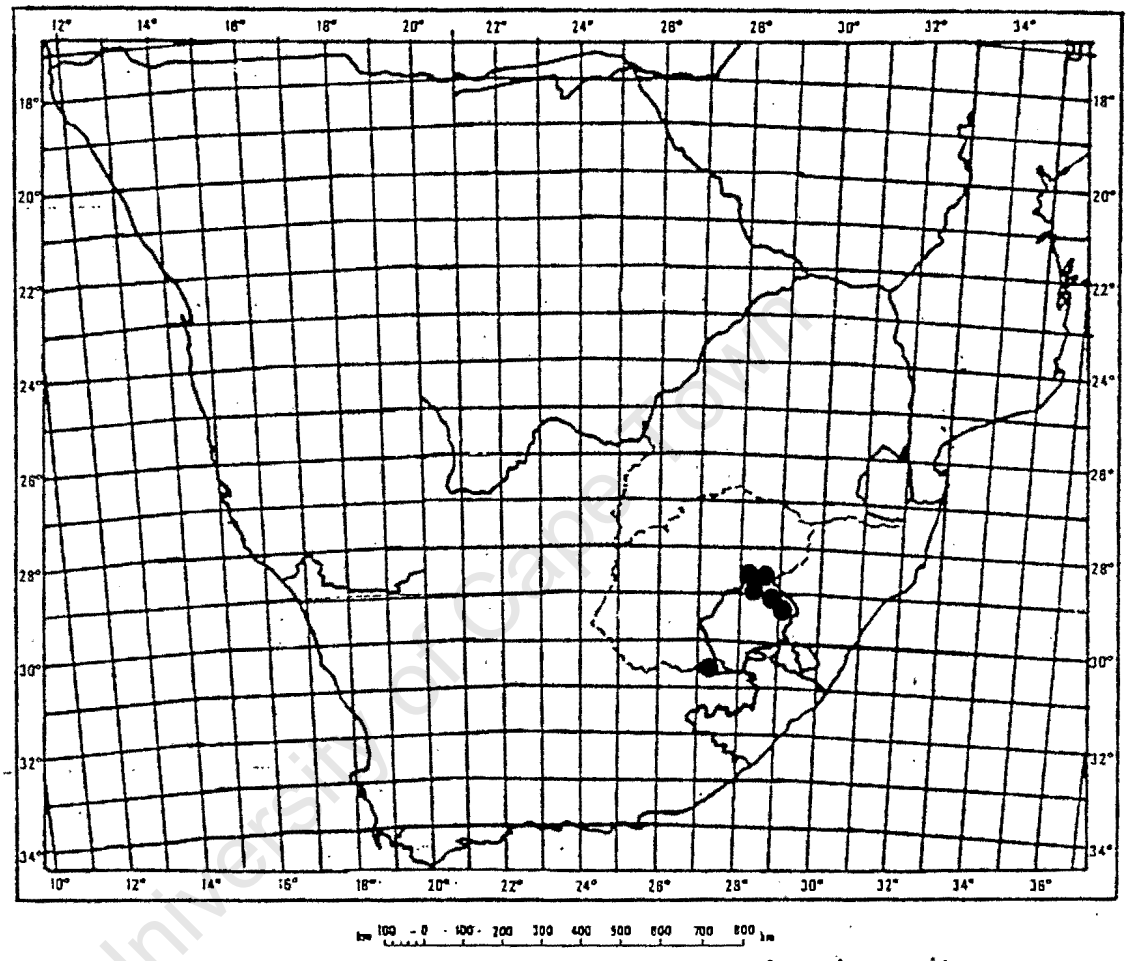


Fig. 2. Known geographical distribution of Deschampsia cespitosa in southern Africa.

Agreement with types

Chippindall (1955) and Clayton (1970) commented that *D. cespitosa* is a polymorphous species which may be represented in F.S.A. by an undescribed taxon. In this study it is confirmed that the local material and the overseas material represent one taxon, *D. cespitosa* as described overseas. It is also confirmed that *D. cespitosa* is a polymorphous species varying mainly in tussock size and leaf length.

Voucher specimens: Hoener 1769 (PRE); du Toit 2233, (PRE).

2. *Deschampsia flexuosa* (L.) Trin. in Mem. Acad. Sci. Petersb., ser. 6, 1:62 (1836); Hubbard, F.T.A.: 93 (1937); Chippindall, Gr. & Past. S.A.: 85 (1955); Clayton, F.T.E.A.: 94 (1970); Clarke, Fl. Europ. 5:226 (1980).

Aira flexuosa L. Sp. Pl.: 65 (1753). Type: s.l. (LINN-Microfiche, BOL.!)

Note: The image that was seen in the microfiche collection of LINN seems to resemble *D. flexuosa* although the morphology could only be superficially examined.

Plants perennial, caespitose, sometimes rhizomatous. Culms slender, erect or curved at base, 5 -- 50cm long; simple with approximately 1 - 2 nodes; surface ribbed, nitid; apical internode exposed. Leaves basal; sheaths tightly rolled on culms, glabrous; leaf blades filiform, convolute, 2 -- 12cm long, 05 - 1.5mm wide, glabrous to scaberulous, setaceous, truncate; margin

glabrous; ligule membranous, deeply lobed, glabrous, 1 -- 2mm long. **Inflorescence** ovate to oblong, not contracted, 1 -- 7cm long, rachis glabrous, nodes 4 - 6; rachis glabrous to scaberulous; branches flexous, in alternate pairs, sometimes lowermost branches unpaired. **Pedicels** erect, not obscured by the spikelets, glabrous or scabrid, apex gradually thickened. **Spikelets** up to 50, ovate, 2 flowered, pale green, sometimes with a tinge of purple; 5.5 -- 5.6mm long. **Glumes** subequal, 5.5 -- 6mm long, lower lanceolate, acute, glabrous, nitid, 1-nerved, upper ovate, acute, glabrous, upper one 3 nerved. **Callus** minutely bearded. **Rachilla** pubescent, lower one missing, upper up to 0.5mm long. **Lemmas** oblong or elliptic, scaberulous, 5 -- 5.5mm long, slightly shorter than the glumes; apex toothed, awned. **Awn** almost basal, geniculate, upper awn 5 -- 6mm long, lower awn 4 -- 5mm long exserted from the spikelets. **Lodicule** slightly fleshy, entire or lobed, scabrid below, 0.6 -- 0.7mm long. **Palea** two-keeled, scabrid, slightly shorter or equal to lemmas. **Anthers** brown, 1.6 -- 2.0mm long.

Leaf Anatomy

Leaf outline: reduced, rounded w-shape. **Ribs and furrows:** present, ribs 3, furrows medium, narrow. No abaxial ribs and furrows. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** median first order vascular bundle and two lateral second order vascular bundles. Vascular bundles 3 or 5, round to oval. All vascular bundles situated in the centre of the blade. Phloem distinct from xylem, slightly lignified, adjoins the inner

vascular bundle sheath. Metaxylem cells conspicuous, in groups of 3 or 4. **Vascular bundle sheath:** double, outer bundle sheath composed of parenchyma cells, more or less isodiametric, abaxial side not covered by the outer bundle sheath, cells smaller than the mesophyll cells, lack chloroplasts. Mestome sheath cells, smaller than the outer bundle sheath cells, inner radial tangential walls thickened. **Sclerenchyma:** a thin interrupted strand on abaxial surface, adjacent to the epidermal cells, and at margins, not well developed, no adaxial sclerenchyma. **Parenchyma girders:** lacking. **Mesophyll:** irregular; cell shape irregular, intercellular spaces infrequent. Lateral cell count more than 4, continuous between bundles. Adaxial epidermal cells smaller than abaxial epidermal cells, abaxial epidermal cells rectangular. Bulliform cells not distinct. Stomata present on adaxial surface,absent on abaxial surface. Cuticle present on abaxial surface, forms a thin layer. Prickles present, few. Festucoid anatomy.

Flowering time: January - March

Distribution, Ecology and Delimitation of species:

D. flexuosa is native to Europe and distributed through to America and throughout Africa. In the F.S.A. region it is only found in Lesotho and the Cape (Fig. 3), in the Grassland biome. This species has become naturalised at high altitudes, in dry to wet sandy loam soil.

Agreement with types

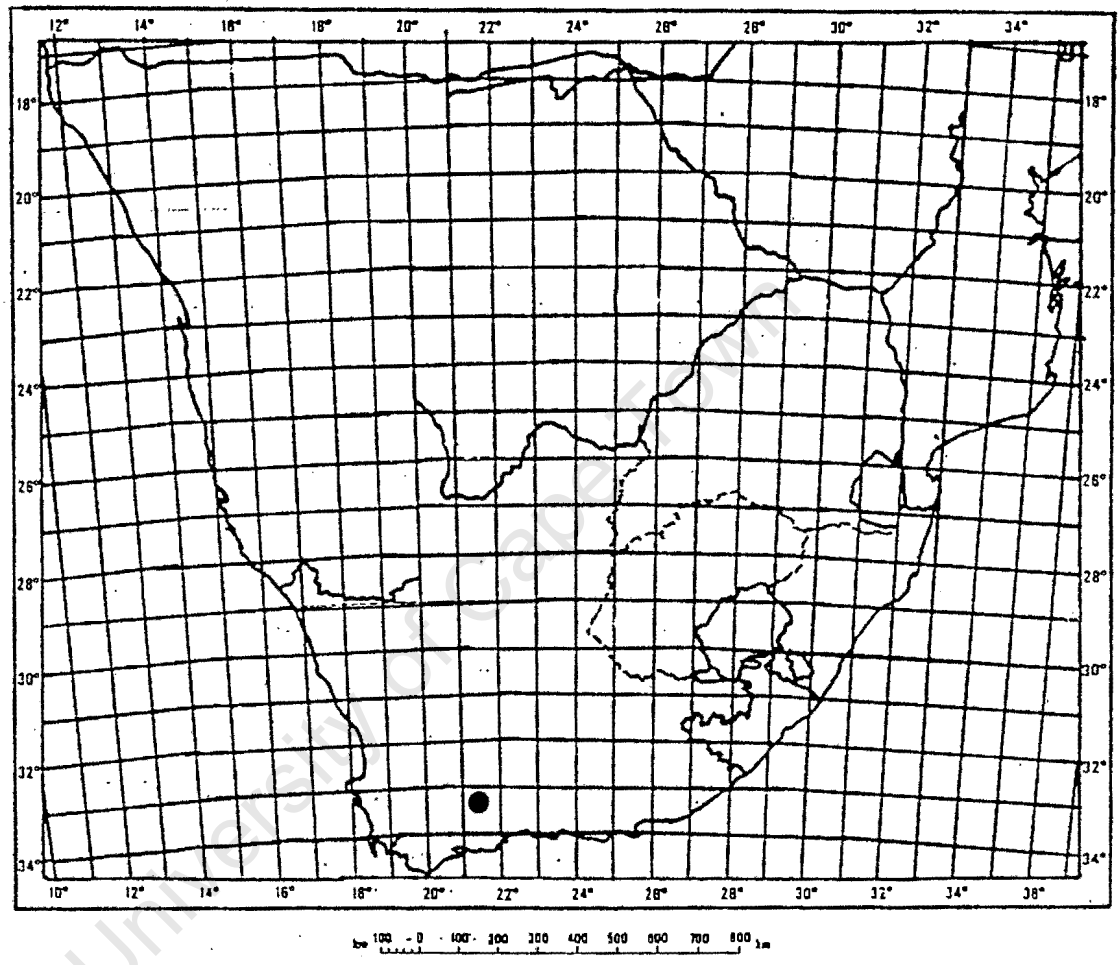


Fig. 3. Known geographical distribution of Deschampsia flexuosa in southern Africa.

Chippindall (1955) states that there is doubt whether *D. flexuosa* represents variety *afromontana* or a distinct variety. De Winter (1979) wrote on a specimen sheet that the specimen concerned represents variety *afromontana* (at Kew) but smaller in size. The examination of the type description and a microfiche copy of the type specimen seem to suggest that variety *afromontana* is a variety of *D. flexuosa*. This variety was described by C.E. Hubbard in 1937 based on material from tropical Africa. It differs from the typical species by having smaller panicles and fewer spikelets. Variety *afromontana* is distinct in Southern African material but in this study it has not been formally described as no infra-specific taxa have been formally recognised.

Voucher specimens: Esterhuysen 33462, (BOL); 28262, (PRE).

2. *Lophochloa* Reichenb., Fl. Germ. Exc.: 42 (1830); Jonsell. in Fl. Europ. 5: 220 (1980)

Festuca Vill. Hist. Pl. Dauph. II: fig. 7. (1775) p.p.;

Koeleria Pers., Syn. Pl.: 1:97 (1805) p.p.; Kunth., Enum. Pl. I: 383 (1833) p.p.; Stapf, F.C. VII: 468 (1899) p.p.; Adamson in Adamson and Salter, Flora of the Cape Peninsula: 84 (1950); Chippindall, Grasses and Pastures of South Africa: 86 (1955) p.p.

Trisetum Pers., Syn. Pl., 97 (1805) p.p.; Kunth., Rev. Gram.: 102 (1829) p.p.; Stapf. in F.C. VII: 470 (1899) p.p.;

Rostraria Trin., Fund. Agrost.: 149 (1822); Clayton and Renvoize, Genera Graminum: 128 (1986).

Trisetaria Forsk., Fl. Aegypt.- Arab. IX: 27 (1775); Chippindall, Grasses and Pastures of South Africa: 84 (1955) p.p.

Plants annual. **Ligule** membranous, with a dentate or lobed apex. **Inflorescence** spiciform to densely so, **Spikelets** numerous, oblong - ovate, 2 - 6 flowered. **Glumes** unequal, 3 - nerved, awnless to mucronate. **Callus** minutely bearded. **Rachilla** scabrid to pubescent. **Lemmas** linear, glabrous or scabrid, 5 nerved. **Lodicules** fleshy at base. **Palea** membranous, 2 keeled, gaping. **Anthers** light to dark brown.

There are two species of this genus in the F.S.A region. *Lophochloa* is closely related to *Koeleria* on gross morphological characteristics. The former, however, is annual while the latter is perennial. Lack of consensus seems to prevail regarding this genus as its species have been placed in at least four genera as above. A discussion of this generic problem is beyond the scope of this study. An indepth study of all the genera concerned is required.

Spikelets 3-4 flowered; upper glume densely pubescent.

.....1.*L. pumila*

Spikelets 3-6 flowered; upper glume glabrous

.....2.*L. cristata*

1. *Lophochloa pumila* (Desf.) Bor, Grasses Burma Ceylon India Pakist: 445 (1960); Jonsell, Fl. Europ.: 5:220, (1980);

Avena pumila Desf. Fl. Atlant. I: 103 (1798).Type: P. Note:

The original publication is not available at BOL so it is not known what the typification was based on. The author's collection is housed at P (Stafleu and Cowan, 1976). *Trisetum pumilum* (Desf.) Kunth., Rev. Gram.: 102 (1805); Enum. Pl. I: 297 (1833); *Trisetum pumilum* (Desf.) Kunth., Rev. Gram.: 102 (1829); Stapf, F.C. VII: 471 (1899). Chippindall, Grasses and Pastures of South Africa: 84 (1955).

Plants annual. **Culms** slender, erect, sometimes geniculate, 4,5 -- 40cm tall, simple with approximately 2 - 4 nodes; culm surface ribbed, nitid; apical internode usually exposed, sometimes covered with sheath. **Leaves** sometimes basal, sheaths tightly rolled on culms, softly hairy or glabrous; leaf blades linear to expanded, 3,5 -- 8cm long and 2 -- 3mm wide, scabrid to softly hairy above, acuminately soft-tipped; ligule lobed, membranous, 1 -- 2mm long, glabrous or slightly hairy above and below. **Inflorescence** spiciform, contracted, continuous, 2 -- 7cm long; nodes 3 - 5, rachis glabrous, scabrid or puberulous; branches conspicuously short, in alternate clusters. **Pedicels** almost obscured by spikelets, glabrous or scabrid, sometimes puberulous; apex gradually thickened. **Spikelets** numerous, oblong - obovate, 3-4 flowered, greyish to green, 2.5 -- 4mm long. **Glumes** unequal, 3- nerved, awnless or shortly awned, lower linear to narrowly ovate, acute, puberulous to pubescent, sometime ciliate on keels, 2.5 -- 4mm long; upper ovate, densely pubescent, 3.5 -- 5mm long. **Callus** minutely bearded. **Rachilla** scabrid to pubescent, 1.5 -- 2mm long. **Lemmas** linear, 2.5 -- 4mm long, upper one slightly shorter than the glumes, glabrous or scabrid, acute, bifid, with

5 prominent nerves, keeled, awned. **Awn** straight, 1.5 -- 4mm long. **Lodicule** fleshy at base, up to 1mm long. **Palea** membranous, 2-keeled, bifid, projecting out of lemma. **Anthers** brown, 0.5 -- 1.5mm long. **Caryopsis** smooth, narrowly lanceolate, 2 -- 2.5mm long, embryo up to 0.5mm long, hilum linear.

Flowering time: September - January

Distribution, Ecology and Delimitation of species:

In the F.S.A. region this species is restricted to the Western Cape Province (Fig. 4). Having been introduced from Europe, *L. pumila* has naturalised in the Fynbos biome in dry, rocky areas, sometimes beneath bushes. This species can be easily confused with *L. cristata* which has less hairy glumes and sometimes a shorter lemma awn. The upper glume of *L. pumila*, however, is always densely pubescent in contrast to that of *L. cristata* which is always glabrous. Hairiness is normally regarded as an unreliable character. In this case the evidence suggests that the presence of hairs on the upper glume of one species and the lack of it on the upper glume of the other species can be relied upon as all the specimens examined consistently confirmed this. This study has proved that the differences in awn length between the two species is not a reliable character as has been used in European keys.

Voucher specimens: Acocks 15020, (PRE); Smook 3657, (PRE).

2. *Lophochloa cristata* (L.) Hyl., Bot. Not.: 355 (1953); Jonsell,

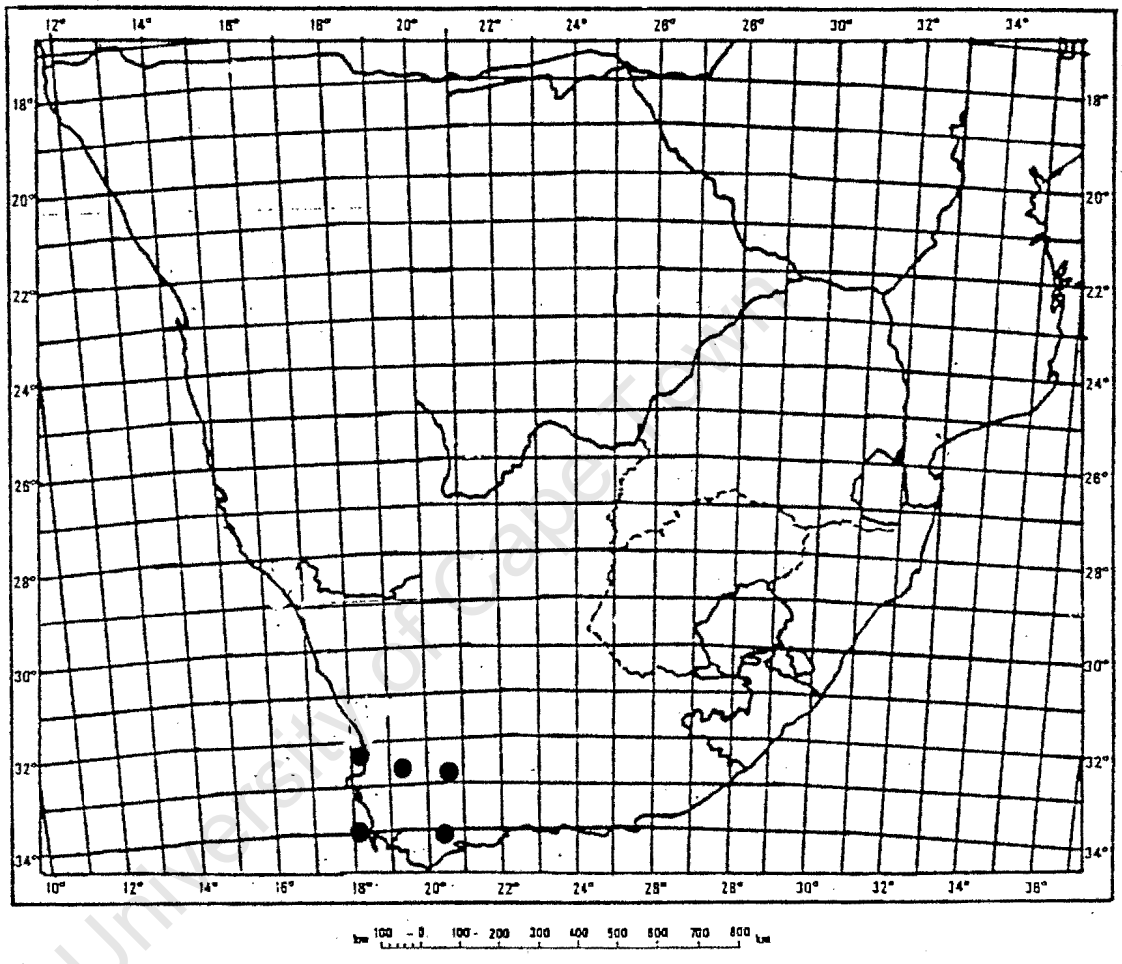


Fig. 4. Known geographical distribution of Lophocloa pumila in southern Africa.

Fl. Europ.: 5:220 (1980).

Aira cristata L., Sp. Pl.: 63 (1753). Note: The typification of this name was probably based on descriptions and illustrations since Linnaeus (1753) cites the following after the phrase name: Bauh. pin. 2. Prodr. 8., Moris. hist. 3. p. 194, S. 8. t. 4. f. 7., Schuech gram. 166.

Festuca phleoides Vill., Hist. Pl. Daulph. Fig. 7: (1798). Note: Most of the author's collections are housed at GRM (Stafleu and Cowan, 1980) so it is likely that the type element or elements are at GRM.

Koeleria phleoides (Vill.) Pers. Syn. Pl. 1: 97 (1805); Kunth., Enum. Pl. I: 383 (1833); Nees, Fl. Afr. Austr.: 428 (1841) p.p.; Durand and Schinz, Consp. Fl. Afr. V: 893 (1895); Stapf, F. C. VII:470 (1899-1900); Adamson in Adamson and Salter, Flora of the Cape Peninsula: 84 (1950); Chippindall, Grasses and Pastures of South Africa: 84 (1955).

Plants annual; loosely tufted. **Culms** slender, erect or curved at base; 5 -- 13,5 cm long, simple with approximately 2-3 nodes; surface smooth or ribbed, nitid; upper half of apical internode exposed. **Leaves** mostly basal; sheaths loosely rolled on culms, glabrous or scaberulous to puberulous; leaf blades expanded, v-shaped, scabrid to villous, 4 -- 12 cm long, up to 2.5mm wide, scabrid to villous, acute; ligule membranous, glabrous with dentate apex, 0.5 -- 1 mm long. **Inflorescence** densely spiciform, continuous, 1 -- 8,5cm long, nodes 4-6, rachis puberulous; branches short, in alternate clusters. **Pedicels** not obscured by spikelets, puberulous to pubescent, apex gradually thickened.

Spikelets numerous, oblong - obovate, 3-6 flowered, pale to dark green, 3-5mm long. **Glumes** subequal, lower glume lanceolate to ovate, glabrous or pubescent, acute, 3 -- 4.5mm long, upper glume linear to ovate, acute, glabrous, 3.5 -- 5mm long. **Callus** minutely bearded. **Rachilla** puberulous, up to 1mm long. **Lemma** linear, glabrous, 2.5 -- 3mm long, acuminate, bifid, 5 veined, ciliate at margins, awned. **Awn** straight, 2.5 -- 3mm long. **Lodicule** fleshy at base, 0.5 -- 1mm long. **Palea** membranous, 2-keeled, glabrous, bifid, conspicuously projecting from lemma. **Anthers** light brown, 1 -- 1.8mm long. **Caryopsis** smooth, narrowly lanceolate, 2 -- 3mm long; embryo up to 0.5mm long, hilum linear.

Leaf Anatomy

Leaf outline: reduced u-shaped, keel not well developed. **Adaxial ribs and furrows:** present between all vascular bundles, ribs 11, medium, slightly wide; furrows deep, narrow. No abaxial ribs and furrows. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** first order vascular bundles alternate with second order vascular bundles, towards the margins first order vascular bundles are replaced by second order vascular bundles, the latter replaced by third order vascular bundles. Vascular bundles 10, round to oval; corresponding to the ribs and situated in the centre of the blade. Phloem distinct from xylem, not lignified, adjoining the inner vascular bundle sheath. Metaxylem cells conspicuous, in groups of 4 or 5. **Vascular bundle sheath:** double, outer bundle sheath composed of parenchyma cells, more or less isodiametric, lacking abaxially, cells smaller than the mesophyll

cells, lacking chloroplasts. Mestome sheath cells smaller than the outer bundle sheath cells, sometimes radially thickened. **Sclerenchyma:** abaxial sclerenchyma strands not always present, when present adjacent to the epidermal cells, adaxial sclerenchyma strands sometimes absent, when present very reduced and adjacent to the upper epidermal cells, sometimes well developed below the median vascular bundle and at the margins.**Parenchyma girders:** lacking. **Mesophyll:** irregular and tending to being radiate, cell shape irregular, intercellular spaces infrequent. Lateral cell count more than 4, continuous between bundles. **Adaxial epidermis:** cells smaller than abaxial epidermal cells. Bulliform cells distinct, large, in groups of three at bases of furrows, stomata present. **Abaxial epidermis:** stomata lacking, cells bigger than adaxial epidermal cells. Cuticle present, forming a thin layer. Anatomy festucoid.

Flowering time: October - December.

Distribution, Ecology and Delimitation of species:

Like *L. pumila* this species of European origin is restricted to the Cape (Fig. 5) in its distribution in the F.S.A. region. It inhabits dry exposed areas, sometimes also moist rocky areas. It has naturalised in the Fynbos biome where it is a weed. This species also occurs in North Africa and India.

Voucher specimen: Cleghorn 3144, (PRE);

3. *Holcus* L., Sp. Pl.: 1047 (1753); Stapf in F.C.: VII: 464 (1899); Stent in Bothalia: 1:284 (1924); Chippindall, Grasses and

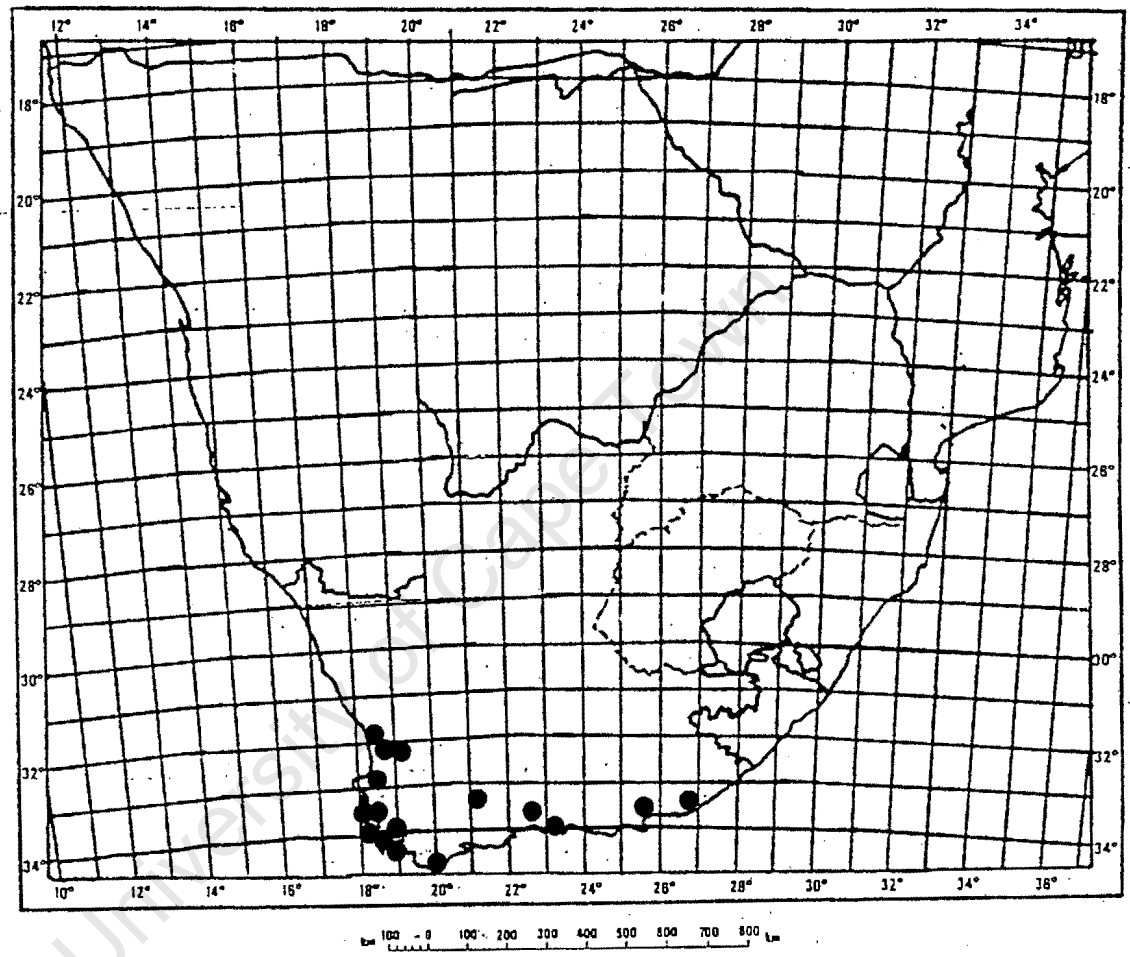


Fig. 5. Known geographical distribution of Lophocloa cristata in southern Africa.

Pastures of South Africa: 87 (1955); Dyer, The Genera of southern African Flowering Plants 2: 834 (1976); Tutin., in Fl. Europ. 5:230 (1980); Clayton and Renvoize, Genera Graminum: 130 (1986).

Plants annuals or perrenials. **Leaves** not basal, ligule lobed, pubescent or scabrid. **Inflorescence** spreading or dense and contracted. **Spikelets** numerous, ovate, 2 flowered. **Glumes** subequal, upper one prominently 3 - nerved, the middle nerve excurrent into an awn, lower 1 nerved. **Callus** sparsely to very sparsely bearded. **Rachilla** internodes glabrous to puberulous. **Lemmas** ovate - oblong, upper lemma with hooked awn, sometimes sterile, lower lemma awnless, coriaceous, lemmas shorter that the glumes. **Lodicules** fleshy at base. **Caryopsis** ellipsoid, hilum linear.

This genus includes six species indigenous in Europe, North Africa, Middle East and Southern Africa. In the F.S.A. region it is represented by two species, one of which is introduced. See Fig. 6 for some of the results. The graph shows that while the two species of this genus appear to be very similar some characters can be used convincingly to distinguish between them. This genus is distinguished from other genera by its hooked awns, lower lemma with bisexual florets, upper male florets and the spikelet that falls as a unit.

Perennial, leaves villous, ligule 1.5 -- 2mm long, upper glume sometimes with an awn up to 1mm long, upper floret usually male

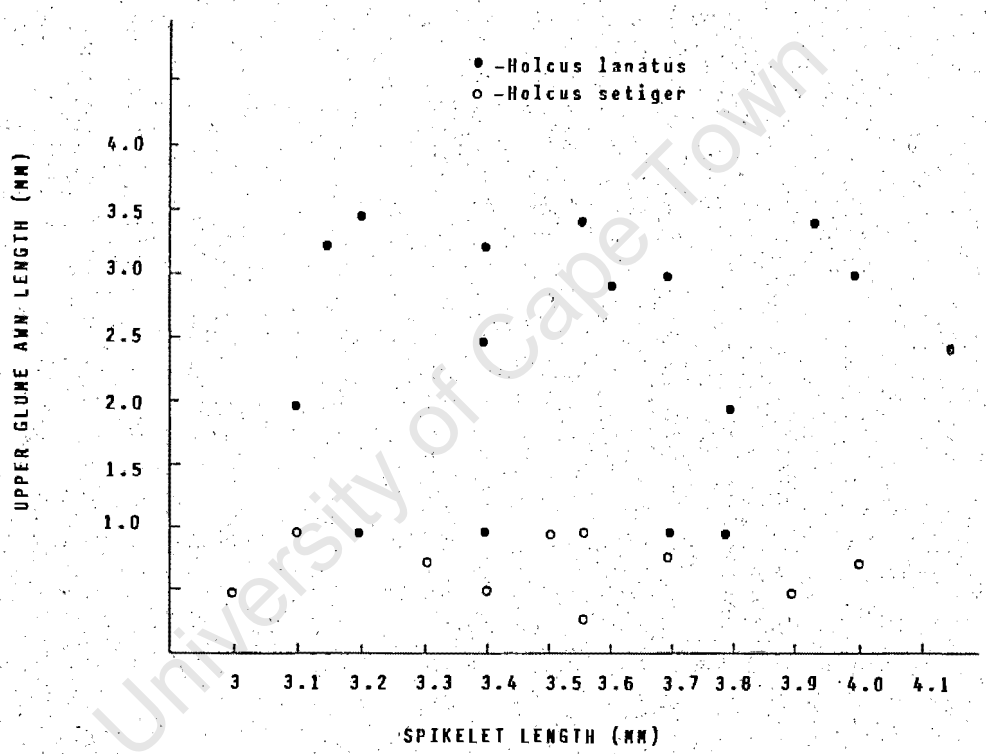


Fig. 6. Scatter diagram showing variation between H. lanatus and H. setiger.

.....1. *H. lanatus*

Annual, leaves puberulous, ligule 1 -- 4.5mm long, upper glume with an awn up to 4mm long, upper floret sterile ...2. *H. setiger*

1. *Holcus lanatus* L., Sp. Pl.: 1048 (1753); Stapf, FC.: 7:465 (1899); Burtt-Davy, Checklist Tvl. & Swaziland: 130 (1911); Stent, Bothalia, 1:284 (1924); Phillips, S.A. Grasses: 237 (1931); Adamson in Adamson and Salter, Flora of the Cape Peninsula: 66 (1950); Hubbard, Grasses: 35 (1954); Chippindall, Grasses and Pastures of South Africa: 87 (1955).

Note: The type specimen is not listed by Savage (1945) and is not in the microfiche collection of the Linnaeus herbarium. Linnaeus (1753) cited Flora Suecica, 67 (1745) and Hortus Cliffortianus after the phrase name. Linnnaes' type description was probably based on Clifford's collection which is house at BM. I did not see the type specimen.

Plants perennial, loosely caespitose. **Culms** erect, sometimes curved at base, 30 -- 100cm long; simple with approximately 5 nodes; surface ribbed, pale; apical internode exposed or sometimes covered with sheath; **Leaves** not basal, sheaths loosely rolled on culms, softly hairy; leaf blades expanded, 5.5 -- 18.5cm long, 1.5 -- 8mm wide, softly hairy, acuminate, soft-tipped or setaceous; margins glabrous; ligule lobed, scabrid above, 1.5 -- 2mm long. **Inflorescence** open and spreading or dense and contracted, 5 -- 13cm long, oblong, ovate, nodes 10 - 17; rachis scabrid to puberulous; branches often short, sometimes swollen at base, arranged in alternate clusters. **Pedicels**

sometimes obscured by spikelets, erect, hairy; apex not thickened. **Spikelets** numerous, ovate, 2 flowered, whitish to dark purple, 3 -- 4mm long. **Glumes** subequal, ovate, truncate, scabrid to villous, more so on keels, 3 -- 4mm long, prominently nerved, upper 3 nerved, lower 1 nerved, the middle nerve excurrent into an awn up to 1 mm long. **Callus** very sparsely bearded. **Rachilla** glabrous, 0.5 -- 1mm, lower curved. **Lemmas** ovate, glabrous, 2.2 -- 5mm long, acuminately bilobed, lemma of upper floret with hooked awn, from upper one third, lower lemma awnless, lemmas shorter than the glumes. **Lodicules** fleshy at base, 0.8 -- 0.9mm long. **Palea** two keeled, ciliate at apex. **Anthers** 1.1 -- 1.7mm long.

Leaf Anatomy

Leaf outline: wide, open, arms horizontal or slightly elevated, keel well developed. **Ribs and furrows:** adaxial ribs and furrows present, sometimes not distinct, ribs 17 - 20, big, wide, furrows very shallow. No abaxial ribs and furrows. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** irregular; first, second, and third order vascular bundles present. Third order vascular bundles frequent towards the margins. Vascular bundles 17 - 20, ovoid to round, corresponding to the ribs, situated in the centre of the blade. Phloem distinct from xylem, not lignified, adjoining the inner vascular bundle sheath. Metaxylem cells conspicuous, in groups of 4 or 5. **Vascular bundle sheath:** double, outer bundle sheath composed of parenchyma cells, more or less isodiametric, abaxial side not covered by the outer

bundle sheath, cells smaller than the mesophyll cells, lacking chloroplasts. Mestome sheath cells smaller than the outer bundle sheath cells, not thickened. **Sclerenchyma:** Abaxial sclerenchyma strands always present, adjacent to the epidermal cells, adaxial sclerenchyma strands sometimes absent, when present adjacent to the upper epidermal cells, not well developed or sometimes well developed below the median vascular bundle. **Parenchyma girders:** abaxial parenchyma girders always present and adaxial parenchyma girders sometimes lacking, sometimes continuous from the lower to the upper epidermal cells, in rows of two's or three's, always associated with vascular bundles. **Mesophyll:** irregular; tending to being radiate, cell shape irregular, intercellular spaces infrequent. Lateral cell count more than 4, continuous between bundles. **Adaxial and abaxial epidermis:** adaxial epidermal cells about equal in size to abaxial epidermal cells. Bulliform cells distinct, large, in groups of three or four at bases of furrows. Stomata present on both surfaces, few on abaxial surface. Cuticle lacking. Prickles present, few on ribs.

Flowering time: November - January

Distribution, Ecology and Delimitation of species:

H. lanatus is widely distributed in its area of origin in Europe. It also occurs in the Mediterranean. In southern Africa it is found in a relatively wide area in Transvaal, Natal, Lesotho and in the Cape (Fig. 7). In these areas it is found in the Savanna, Fynbos and Forest biomes. This species has become naturalised in the Cape and in Natal.

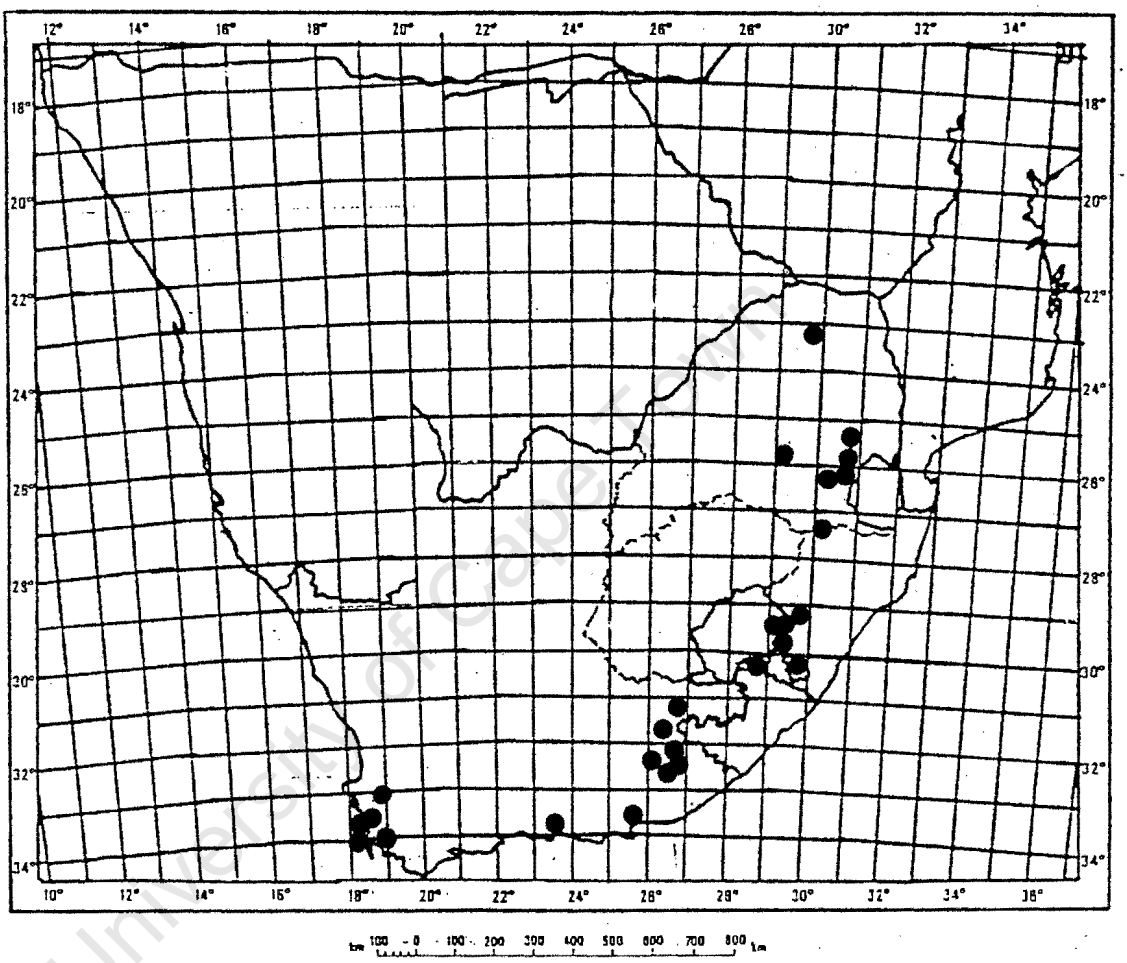


Fig. 7. Known geographical distribution of Holcus lanatus in southern Africa.

Although *H. lanatus* is locally common, it is ecologically restricted to vleis, damp sheltered places on sandy soils. It is occasionally found on nutrient rich soils. This species is occasionally cultivated for pasture purposes.

Voucher specimens: Smook 4878, (PRE); Dyer 6277, (PRE).

2. *Holcus setiger* Nees, Linnaea 7: 278 (1832); Stapf, FC. 7: 464 (1899); Adamson in Adamson and Salter, Flora of the Cape Peninsula: 66 (1950); Chippindall, Grasses and Pastures of South Africa: 87 (1955). Type: Hottentots Holland, Ecklon herb. s.n. (Holo). Ecklon's collections are wildey dispersed. However, most of his collections were acquired by Ferdinand von Mueller and is now presumably at MEL. (Stafleu and Cowan, 1976).

Plants annual, several stemmed. **Culms** erect, sometimes curved at base, 15 -- 30cm long, simple with approximately 5 - 7 nodes; surface ribbed, nitid; apical internode sometimes exserted. **Leaves** not basal; sheaths loosely rolled on culms, puberulous to hairy, sheath mouth bearded; leaf blades expanded, 2.5 -- 140cm long and 1 -- 8mm wide, puberulous above and below, acute, soft-tipped; ligule deeply lobed, pubescent, 1 -- 4.5mm long. **Inflorescence** open or dense and contracted, 7 -- 15cm long, spiciform to oblong; rachis puberulous to villous, nodes 10 - 17; branches often short, sometimes swollen at base and obscured by spikelets, arranged in alternate clusters. **Pedicels** erect or recurved , sometimes obscured by the spikelets; apex not thickened. **Spikelets** numerous, ovate - oblong, 2 flowered, light green with a yellow tinge, 3 -- 4mm long. **Glumes** subequal, ovate,

obtuse, scabrid to villous, more so on keels, pale green, 3 -- 4mm long, prominently 3 nerved on upper glume, middle nerve excurrent into an awn, up to 4mm long, 1 nerved on lower glume, excurrent into an awn up to 1mm long. **Callus** sparsely bearded. **Rachilla** glabrous to puberulous, 0.5 -- 1mm. **Lemmas** ovate - oblong, bilobed, glabrous, 1 -- 2.5mm long; upper lemma with a hooked awn inserted in the upper third, sterile, narrower and shorter than the lower; lower lemma awnless, usually bisexual, rigid, almost leathery, shorter than the glumes. **Lodicules** sometimes fleshy at base, 0.7 -- 0.8mm long. **Palea** two keeled, glabrous, equal to or slightly shorter than the lemma. **Anthers** 0.5 - 0.9mm long.

Leaf Anatomy

Leaf outline: wide, open, arms horizontal or slightly elevated, keel not well developed. **Ribs and furrows:** adaxial ribs and furrows present, sometimes not distinct, ribs 14 - 18, big, wide, slightly rounded; furrows wide and very shallow. No abaxial ribs and furrows. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** irregular; first, second, and third order vascular bundles present. Third order vascular bundles frequent towards the margins. Vascular bundles vary, 12 - 17, ovoid to round, corresponding to the ribs, situated in the centre of the blade. Phloem distinct from xylem, not lignified, adjoining the inner vascular bundle sheath. Metaxylem cells conspicuous, in groups of 4 or 5. **Vascular bundle sheath:** double, outer bundle sheath composed of parenchyma cells, more or less isodiametric, abaxial

side not covered by the outer bundle sheath, cells smaller than the mesophyll cells, lacking chloroplasts. Mestome sheath cells smaller than the outer bundle sheath cells, not thickened. **Sclerenchyma:** Abaxial sclerenchyma strands always present, adjacent to the epidermal cells, adaxial sclerenchyma strands sometimes absent, when present adjacent to the upper epidermal cells, not well developed or sometimes well developed below the median vascular bundle. **Parenchyma girders:** abaxial parenchyma girders always present, adaxial parenchyma girders sometimes lacking, sometimes continuous from the lower to the upper epidermal cells, in rows of two's or three's, always associated with vascular bundles. **Mesophyll:** irregular; tends towards radiate, cell shape irregular, intercellular spaces infrequent. Lateral cell count more than 4, continuous between bundles. **Adaxial and abaxial epidermis:** adaxial epidermal cells about equal in size to abaxial epidermal cells. Bulliform cells distinct, large, in groups of three or four at bases of furrows. Stomata present on both surfaces, few on abaxial surface. Cuticle lacking. Prickles present, few on ribs.

Flowering time: November to January

Distribution, Ecology and Delimitation of species:

Holcus setiger is indigenous to the F.S.A region where it is found in Natal and the Cape (Fig. 8). It is locally common in damp or sheltered places on sandy soils to sandy loam soils in the Fynbos and Savanna biomes. These species are characterised by expanded leaf blades that gradually taper to a point. The leaves

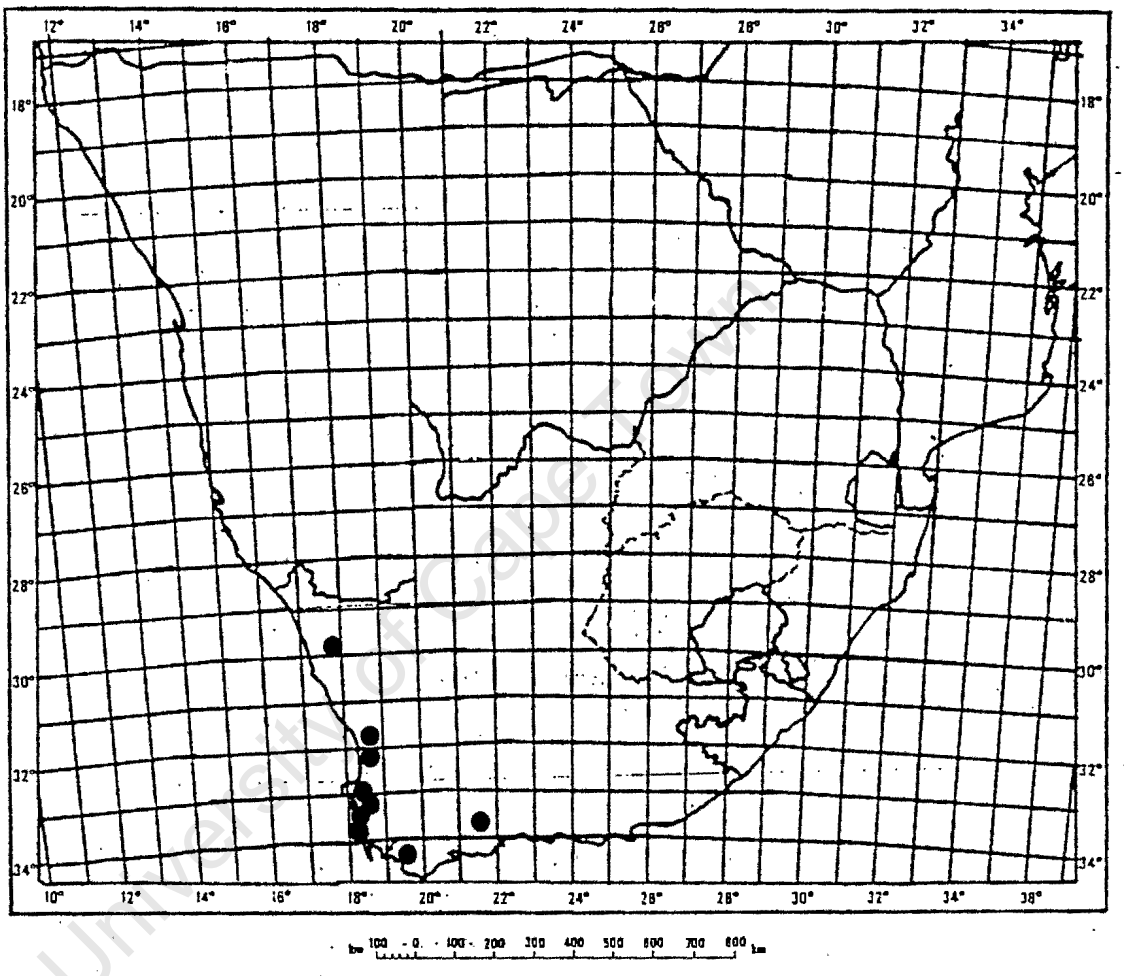


Fig. 8. Known geographical distribution of Holcus setiger in southern Africa.

are softly hairy in *H. lanatus*, more densely hairy than *H. setiger*. The former is easily distinguished from its relative by the awned upper glume while the lower glume lacks awns or when present shorter that the upper awn. In *H. setiger* the upper glume has a conspicuosly longer awn than that of *H. lanatus*. *H. setiger* is further delimited from *H. lanatus* by its sterile upper floret.

Although these species are variable in glume and lemma awn length, they are distinct species which cannot be confused with each other. *Holcus setiger* is annual while *H. lanatus* is perennial.

Chippindall (1955) comments that a form of *H. setiger* from George, in the Southern Cape and from Kamiesberg in Namaqualand is exceptionally weak, slender and delicate. Specimens examined in this study show an apparent continuity in their variation. See Fig. 6.

Voucher specimens: Acocks 22966, PRE, Taylor 3489, (PRE).

4. *Avena* L., Sp. Pl.: 97 (1753); Stapf. in F.C. VII:477 (1899); Launert in FZ. 10,1:74 (1971); Adamson in Adamson and Salter, Flora of the Cape Peninsula: 69 (1950); Chippindall, Grasses and Pastures of South Africa: 80 (1955); Dyer, The Genera of southern African Flowering Plants 2: 835 (1976); Rocha Afonso in Fl. Europ. 5:206 (1980); Clayton and Renvoize, Genera Graminum: 124 (1986).

Plants annual. Leaves sometimes basal; ligule lobed,

scabrid. **Inflorescence** open, spreading, sometimes contracted, ovate to oblong, sometimes drooping to one side. **Spikelets** numerous. **Glumes** subequal. **Callus** sparsely to densely bearded. **Rachilla** glabrous, scaberulous, sometimes puberulous. **Lemmas** ovate to narrowley lanceolate, biaristulate, awned. **Lodicules** fleshy at base. **Anthers** brown.

A genus of twenty-five species, mainly of Mediterranean and Middle East origin but extending into northern Europe. This genus is widely introduced to other regions including the F.S.A. region. In this region it is represented by four species. *Avena* can be easily distinguished in the F.S.A. region. However some of the species within the genus closely resemble each other making it difficult to distinguish between them.

This is a relatively uniform genus. This study revealed that the character suites are not consistent, with one or two of the characters used varying between specimens. Fig. 9 shows some of the differences between species. This made it difficult to construct keys for identification purposes. Rocha Afonso (1980) relied mainly on the manner of spikelet break-up at maturity for identification.

While this is acceptable, it implies that it is impossible to identify fresh plants based on other characters during active growth. A combination of certain characters can be used to identify the species in this genus inspite of its uniformity.

1. Rachilla disarticulating above glumes but not between florets at maturity, lemma teeth 1-1.5mm long.....4. *A. sterilis*

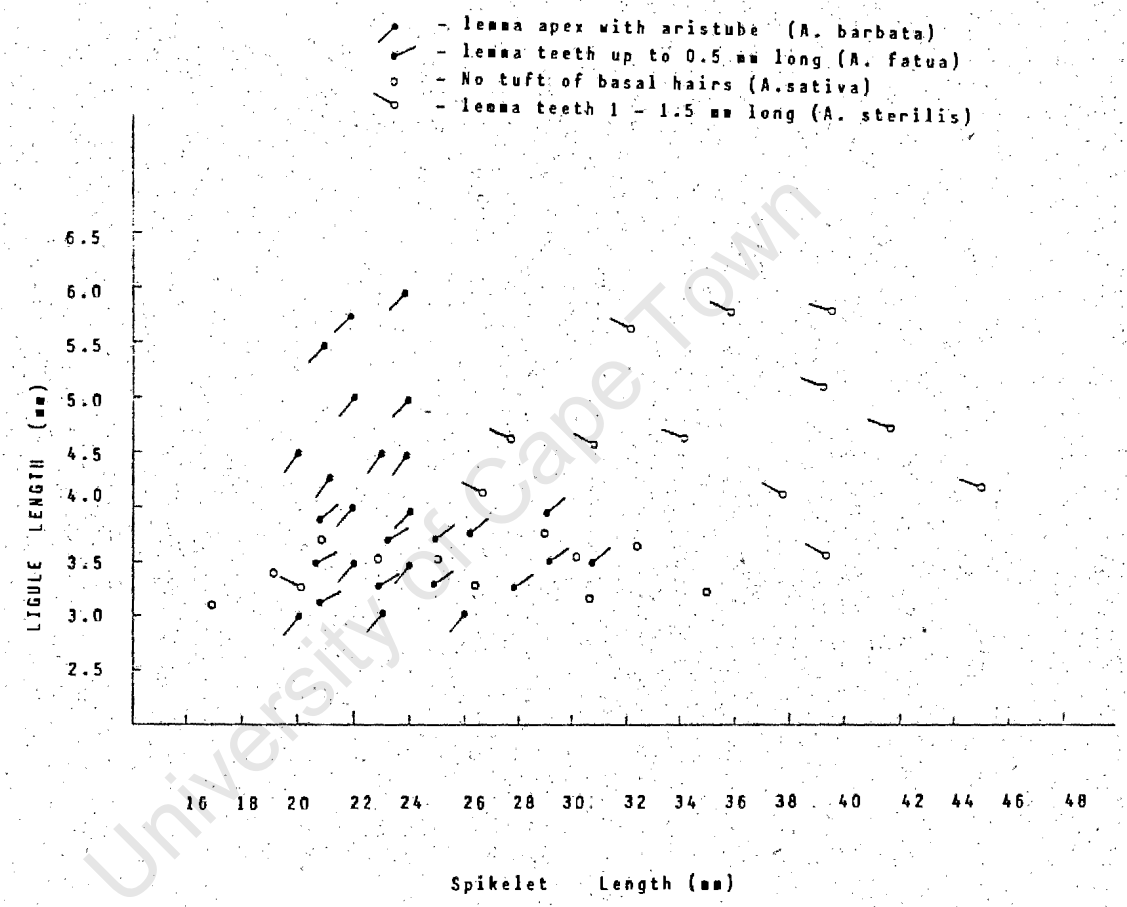


Fig. 9. Scatter diagram showing variation in Avena with A. fatua, A. barbata, A. sterilis and A. sativa.

1. Rachilla disarticulating above glumes and between florets at maturity, lemma apex biaristulate.....1. *A. barbata*

2. Lemma villous up to awn insertion, apex bidentate with teeth up to 0.5mm long.....2. *A. fatua*

2. Lemma glabrous or sparsely hairy, apex emarginate or shortly notched .....3. *A. sativa*

1. *Avena barbata* Pott ex Link in Schrader, Jour. fur die Bot. 1799 (2): 315 (1800); Stapf in FC. 7:480 (1899); Burtt-Davy, Cheklist Tvl & Swaziland: 130 (1911); Adamson in Adamson and Salter, Flora of the Cape Peninsula: 69 (1950); Chippindall, Grasses and Pastures of South Africa: 81 (1955).
Type: Europe. The details of the type specimen/s are unknown. However the author's type specimens are housed at LE so it is possible that it is where this particular type specimen is housed.

Plants annual, several stemmed. **Culms** erect or curved at base, 30cm -- 130cm long; simple with approximately 3 nodes; surface ribbed or smooth, nitid; apical internode exposed, rarely covered with sheath. **Leaves** usually few; sheaths tightly rolled on culms, glabrous; leaf blades expanded, 7 -- 30cm long, 3 -- 10mm wide; glabrous, acuminate, soft-tipped, margin scabrid; ligule lobed, scabrid above, 3 -- 6mm long. **Inflorescence** open, spreading, drooping to one side, 5 -- 30cm long, nodes 7 - 12, rachis glabrous; branches arranged in alternate pairs or clusters. **Pedicels** not obscured by spikelets, recurved, scabrid, gradually thickened. **Spikelets** pendulous, numerous, lanceolate, 2 flowered,

pale to dark green, 18 -- 26mm long. **Glumes** subequal, acuminate, glabrous, nitid, margins hyaline, 18 -- 26mm long, 9 nerved. **Callus** densely bearded. **Rachilla** glabrous, disarticulating between florets at maturity, lower one missing, upper up to 2.5mm long. **Lemmas** narrowly lanceolate, villous up to awn insertion, acuminate, acute, 18 -- 25mm long, apex biaristulated, aristulae 3 -- 5mm long, lemmas shorter than the glumes, awned. **Awns** arising from the middle of lemma, geniculate, 33 -- 45mm long. **Lodicules** fleshy at base, 1.5 -- 2mm long. **Palea** two keeled, ciliate at margins, shorter than the lemmas. **Anthers** 3 - 4 mm long.

Leaf Anatomy

Leaf outline: wide, open, arms horizontal, keel well developed. **Ribs and furrows:** adaxial ribs and furrows present, sometimes not distinct, ribs 15 - 18, big, wide, furrows very shallow. No abaxial ribs and furrows. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** irregular; first, second, and third order vascular bundles present, random. Third order vascular bundles frequent towards the margins. Vascular bundles 17 - 20, round to oval, corresponding to the ribs, situated in the centre of the blade. Phloem distinct from xylem, not lignified, adjoining the inner vascular bundle sheath. Metaxylem cells conspicuous, in groups of 4 or 5. **Vascular bundle sheath:** double, outer bundle sheath composed of parenchyma cells, more or less isodiametric, abaxial side not covered by the outer bundle sheath, cells smaller than the mesophyll cells, lacking

chloroplasts. Mestome sheath cells smaller than the outer bundle sheath cells, not thickened. **Sclerenchyma:** abaxial sclerenchyma strands always present, inconspicuous, adjacent to the epidermal cells, adaxial sclerenchyma strands sometimes absent and when present adjacent to the upper epidermal cells, not well developed or sometimes well developed below the median vascular bundle. **Parenchyma girders:** adaxial parenchyma girders always present and sometimes lacking abaxially, sometimes continuous from the lower to the upper epidermal cells, in rows of two's or three's, always associated with vascular bundles. **Mesophyll:** irregular; tending to being radiate, cell shape irregular, intercellular spaces infrequent. Lateral cell count more than 4, continuous between bundles. **Epidermis:** Adaxial epidermal cells smaller than the abaxial. Bulliform cells distinct, large, in groups of four to five at bases of furrows. Stomata present on both surfaces, few on the abaxial side. Cuticle sometimes lacking , sometimes a very thin layer.

Flowering time: August - December

Distribution, Ecology and Delimitation of species:

This species is locally dominant in Natal and in the Cape (Fig. 10) where it occurs in the Savanna and Fynbos biome respectively. It grows in waste and disturbed areas, on roadsides and in sandy soil. *A. barbata* is, although variable distinct from the other species. Members of this species can only be separated from other species by the unique presence of aristulae. These awn-like lobes sometimes have a setum each. In Europe the presence and absence

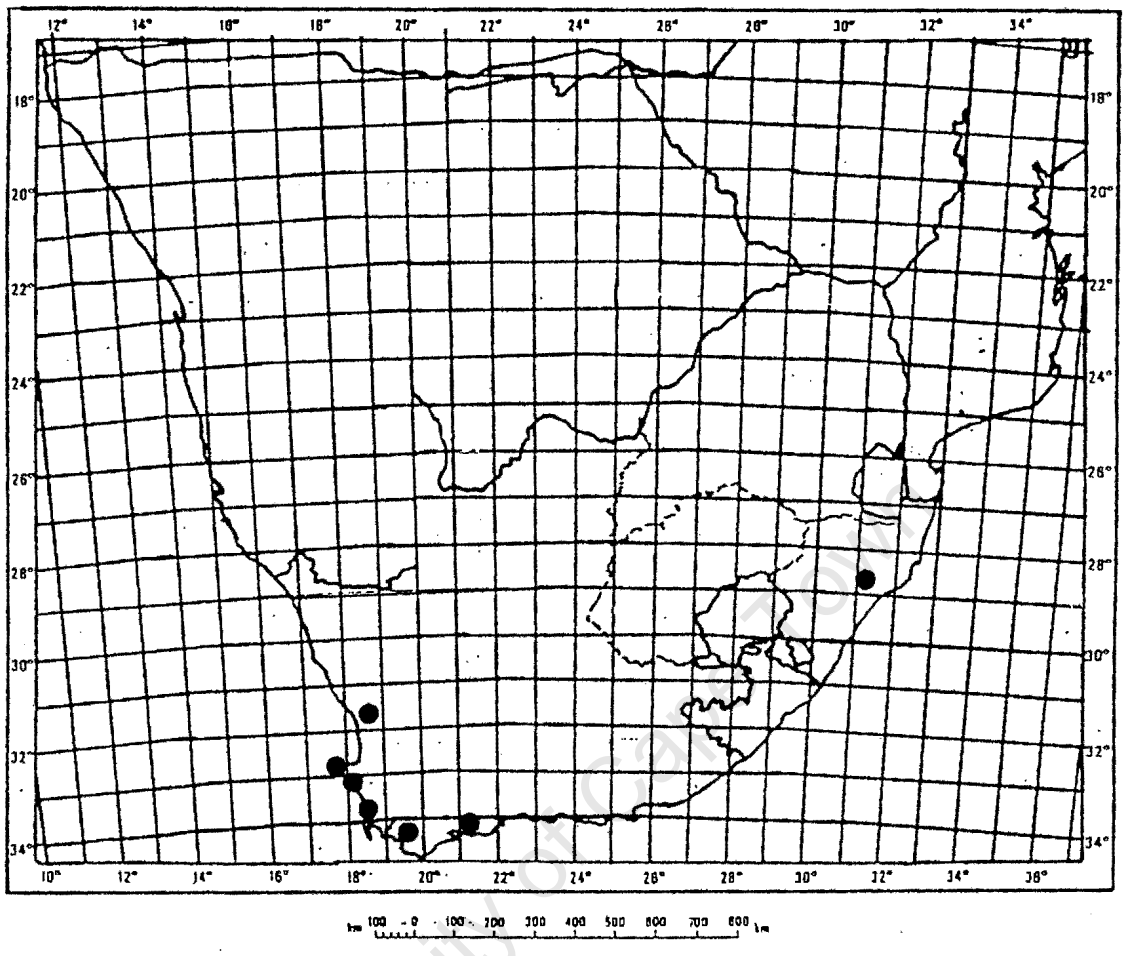


Fig. 10. Known geographical distribution of Avena barbata in southern Africa.

of a lateral seta distinguishes between two subspecies. The typical form lacks the lateral seta while *A. barbata* subsp. *atherantha* has aristulae each with a lateral setum. In the F.S.A. region these subspecies have not been recognised due to the lack of enough material to justify the delimitation. However, some specimens with these differences were observed.

The glume and spikelet lengths vary so widely that they cannot be used effectively as a taxonomic character at this level. However this character can always be used in combination with the presence or absence of aristulae and two florets. The number of florets is consistently two in this species. The number of florets, glumes that are longer than the florets and the basal tuft of white hairs on the spikelet make this species typical of the genus *Avena*.

Voucher specimens: Branch 7, (NBG); Crook 2272, (NBG); Gubb 114, (NBG).

2. *Avena fatua* L., Sp. Pl.: 80 (1753); Stapf in FC. 7:479 (1899); Adamson in Adamson and Salter in Flora of the Cape Peninsula: 69 (1950); Chippindall, Grasses and Pastures of South Africa: 81 (1955); Clayton, F.T.E.A.: 82 (1970); Launert, FZ.: 74 (1971). Type: s.l. (holo. LINN - Microfiche, BOL.!)

Plants annual, single to sveral stemmed. **Culms** erect or curved at base, 25 -- 70cm long, simple with approximately 4 nodes; surface ribbed, nitid; apical internode sometimes exposed. **Leaves** not basal; sheath loosely rolled, glabrous, sometimes scaberulous; leaf blades expanded, 5 -- 28cm long; 3 -- 8mm wide, glabrous,

sometimes scaberulous, acute, soft-tipped; margin scabrid; ligule lobed, scabrid above, 3 - 4mm long. **Inflorescence** open, spreading, broadly ovate, 10 -- 35cm long, nodes 6-10, rachis glabrous to scabrid; branches in alternate pairs or clusters. **Pedicels** not obscured by spikelets, recurved, scabrid; apex gradually thickened. **Spikelets** numerous, ovate or lanceolate, 2 to 4 flowered, pale or dark green, 18 -- 32mm long. **Glumes** subequal, lanceolate, acuminate, glabrous, nitid, margins hyaline, 18 -- 32mm long, 9 or 10 nerved. **Callus** densely bearded. **Rachilla** glabrous, sometimes scabrid, up to 1.5mm long, disarticulating between florets at maturity. **Lemma** ovate - lanceolate, 13 -- 29mm long, acuminate, toothed at apex, teeth up to 0.5mm long, shorter than glumes, hairy up to awn insertion, hairs usually brownish; awned. **Awn** geniculate, arising from the middle of lemma, 25 -- 90mm long. **Lodicule** sometimes fleshy at base, 1.7 - 2mm long. **Palea** two-keeled, ciliate at margins, slightly shorter than lemma. **Anthers** 3.9 - 4.2mm long.

Leaf Anatomy

Leaf outline: open, wide, expanded and flat, arms horizontal or slightly elevated, keel well developed. **Ribs and furrows:** adaxial and abaxial ribs and furrows present between all vascular bundles; adaxial ribs more pronounced than the abaxial ones; ribs 40 - 48, big, slightly wide, furrows shallow, wide. **Median vascular bundle:** not structurally distinct from the lateral first order vascular bundles. **Vascular bundle arrangement:** vascular bundles vary in number, 28 - 34 first order vascular bundles, 10 or 12 second order vascular bundles between

consecutive first order vascular bundles, 3 - 5 third order vascular bundles, vascular bundles associated with the ribs, all vascular bundles situated in the centre of the blade. **Vascular bundle structure:** first order vascular bunldes almost rounded, slightly oval, second order vascular bundles round, with a distinct phloem and xylem, phloem not lignified, adjoins the inner vascular bundle sheath, metaxylem cells conspicuous, in groups of 5 or 6. **Vascular bundle sheath:** double, outer bundle sheath composed of more or less isodiametric parenchyma cells, interrupted on the abaxial side, cells smaller than the mesophyll cells, lacking chloroplasts; mestome sheath cells smaller than the outer bundle sheath cells, not thickened. **Sclerenchyma:** Adaxial and abaxial sclerenchyma strands present, adjacent to the upper and lower epidermis respectively, not well developed adjacent to the third order vascular bundles. **Parenchyma** girders: present, sometimes continuous from the lower to the upper epidermis, in rows of two or three, always associated with vascular bundles, abaxial parenchyma girders not always present, this follows an irregular pattern, not associated with the third order vascular bundles. **Mesophyll:** irregular; intercellular spaces frequent, lateral cell count more than 4, continuous between bundles. **Epidermis:** adaxial epidermal cells not distinct from abaxial epidermal cells, not thickened, bulliform cells distinct on adaxial epidermis, large, in groups of three; lacking on abaxial surface. No macrohairs. Stomata present on both surfaces. Cuticle a very thin layer.

Flowering time: August - November

Distribution, ecology and delimitation of species:

This species is found in the Transvaal, Cape, Natal, O.F.S. and Lesotho, (Fig. 11). With its origin in Europe this weed is found outside the F.S.A. region in North Africa, western and central Asia and East Africa from Kenya and Zimbabwe (Clayton, 1970). It grows on disturbed and waste places, roadsides and in sandy soil. *A. fatua* is not always easy to distinguish from *A. sterilis* during active growth. However at maturity the rachilla of *A. fatua* disarticulates above the glumes and between the florets while in *A. sterilis* the rachilla disarticulates above the glumes but not between the florets.

Voucher specimens: Snijman 36, (NBG); Henderson 1315, (NBG).

3. *Avena sativa* L., Sp. Pl.: 79 (1753); Nees, Fl. Afr. Austr.: 351 (8141); Stapf in FC. 7:478 (1899); Burtt- Davy, Checklist Tvl & Swaziland: 130 (1911); Adamson in Adamson and Salter, Flora of the Cape Peninsula: 69 (1950); Hubbard, Grasses: 211 (1954); Chippindall, Grasses and Pastures of South Africa: 81 (1955); Clayton, F.T.E.A.: 82 (1970); Launert, FZ. 10(1): 74 (1971). Type: s.leg., s.n. (holo. LINN - Microfiche, BOL.!).

Plants annual,single to several stemmed. **Culms** sub-robust, erect or curved at base, 35 -- 105cm tall, simple with approximately 3 - 4 nodes; surface ribbed, nitid; apical internode sometimes exposed. **Leaves** sometimes basal; sheath loose, glabrous; leaf blades expanded, 10 -- 40cm long, 3 -- 9mm wide; glabrous, acute, soft tipped, margins scabrid; ligule scabrid above, lobed,

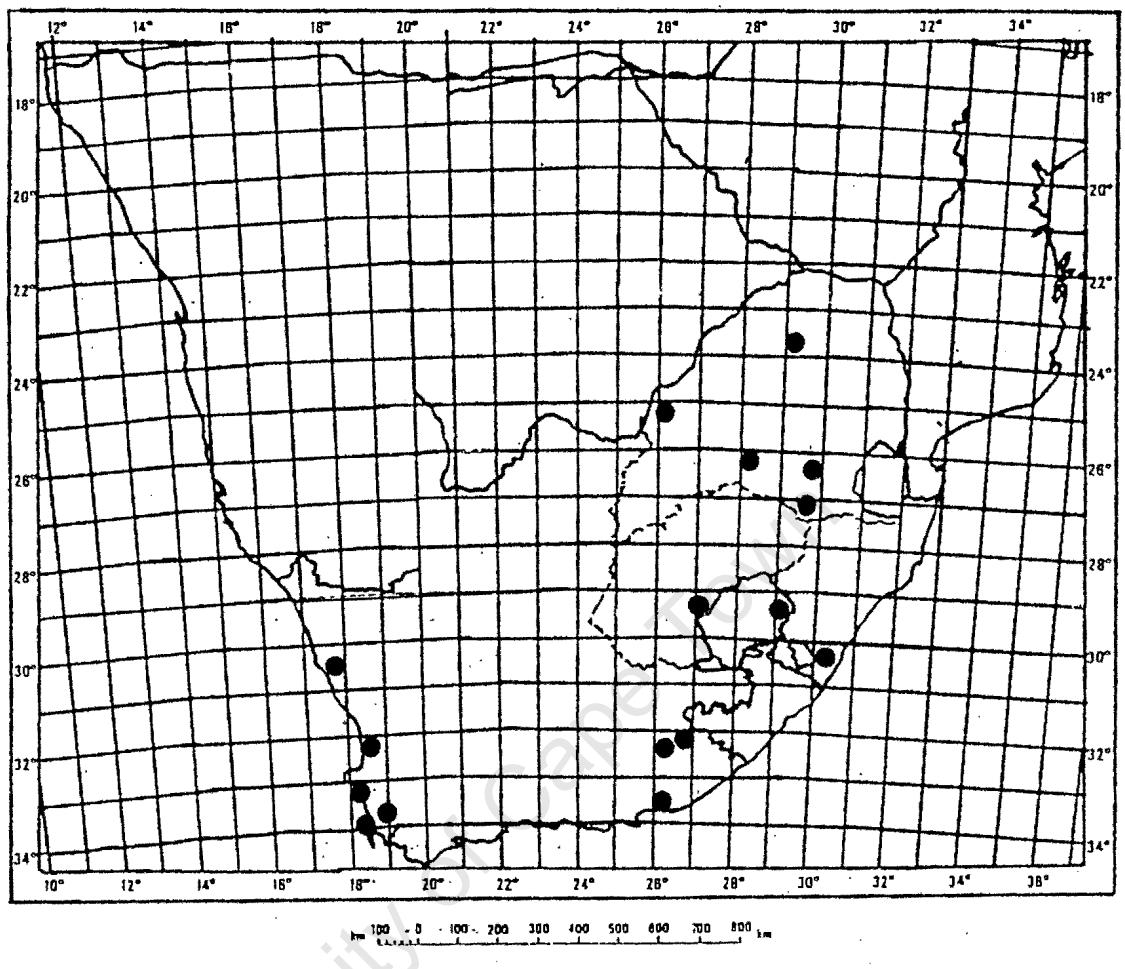


Fig. 11. Known geographical distribution of Avena fatua in southern Africa.

3 -- 4mm long. **Inflorescence** open, spreading or sometimes contracted, drooping to one side, ovate - oblong, 15 -- 35cm long, nodes 5 - 10, rachis glabrous, sometimes scabrid; branches in alternate pairs or clusters. **Pedicels** not obscured by spikelets, sometimes recurved, scabrid, gradually thickened. **Spikelets** numerous, lanceolate - linear, 2 - 3 flowered, bright green, 17 -- 35mm long. **Glumes** subequal, lanceolate, acuminate, glabrous, nitid, margins hyaline, 17 -- 35mm long, 9 - 10 nerved. **Callus** sparsely hairy or glabrous. **Rachilla** glabrous or puberulous, not disarticulating at maturity. **Lemma** narrowly lanceolate, 14 -- 25mm long, emarginate or shortly notched, shorter than the glumes, awnless or awned from the middle. **Awn** (when present) almost straight, 15 -- 40mm long. **Lodicule** fleshy at base, lobed, 1.2 -- 1.6mm. **Palaea** membranous, two keeled, ciliate at margins. **Anthers** 2.3 -- 4mm.

Leaf Anatomy

Leaf outline: wide, open, arms horizontal, keel well developed. **Ribs and furrows:** adaxial ribs and furrows present, sometimes not distinct, ribs 16 - 19, big, wide, furrows very shallow, flat above the keel. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** irregular; first, second and third order vascular bundles present. Third order vascular bundles frequent towards the margins. Vascular bundles 17 - 20, round to oval, corresponding to the ribs, situated in the centre of the blade. Phloem distinct from xylem, not lignified, adjoining the inner vascular bundle sheath. Metaxylem cells conspicuous, in groups of

4 or 5. **Vascular bundle sheath:** double, outer bundle sheath composed of parenchyma cells,more or less isodiametric, abaxial side not covered by the outer bundle sheath, cells smaller than the mesophyll cells, lacking chloroplasts. Mestome sheath cells smaller than the outer bundle sheath cells, not thickened. **Sclerenchyma:** abaxial and adaxial sclerenchyma strands not always present, adjacent to the epidermal cells, not well developed, sometimes well developed below the median vascular bundle. **Parenchyma girders:** adaxial parenchyma girders always present, abaxial sometimes lacking, sometimes continuous from the lower to the upper epidermal cells, in rows of two or three, always associated with vascular bundles. **Mesophyll:** irregular; tending to being radiate, cell shape irregular, intercellular spaces infrequent. Lateral cell count more than 4, continuous between bundles. **Epidermis:** Adaxial epidermal cells smaller than abaxial epidermal cells. Bulliform cells distinct, large, in groups of four to five at bases of furrows. Stomata present on both surfaces, few on abaxial side. Cuticle sometimes lacking, sometimes a very thin layer.

Flowering time: September - November

Distribution, Ecology and Delimitation of species:

Avena sativa occurs in the Transvaal and the Cape, (Fig. 12) in the Savanna and Fynbos biome respectively. With its origin in Europe this species is a weed in the F.S.A. region where it grows in waste and disturbed areas and on roadsides where it is locally common. *A. sativa* can be distinguished from other species by its

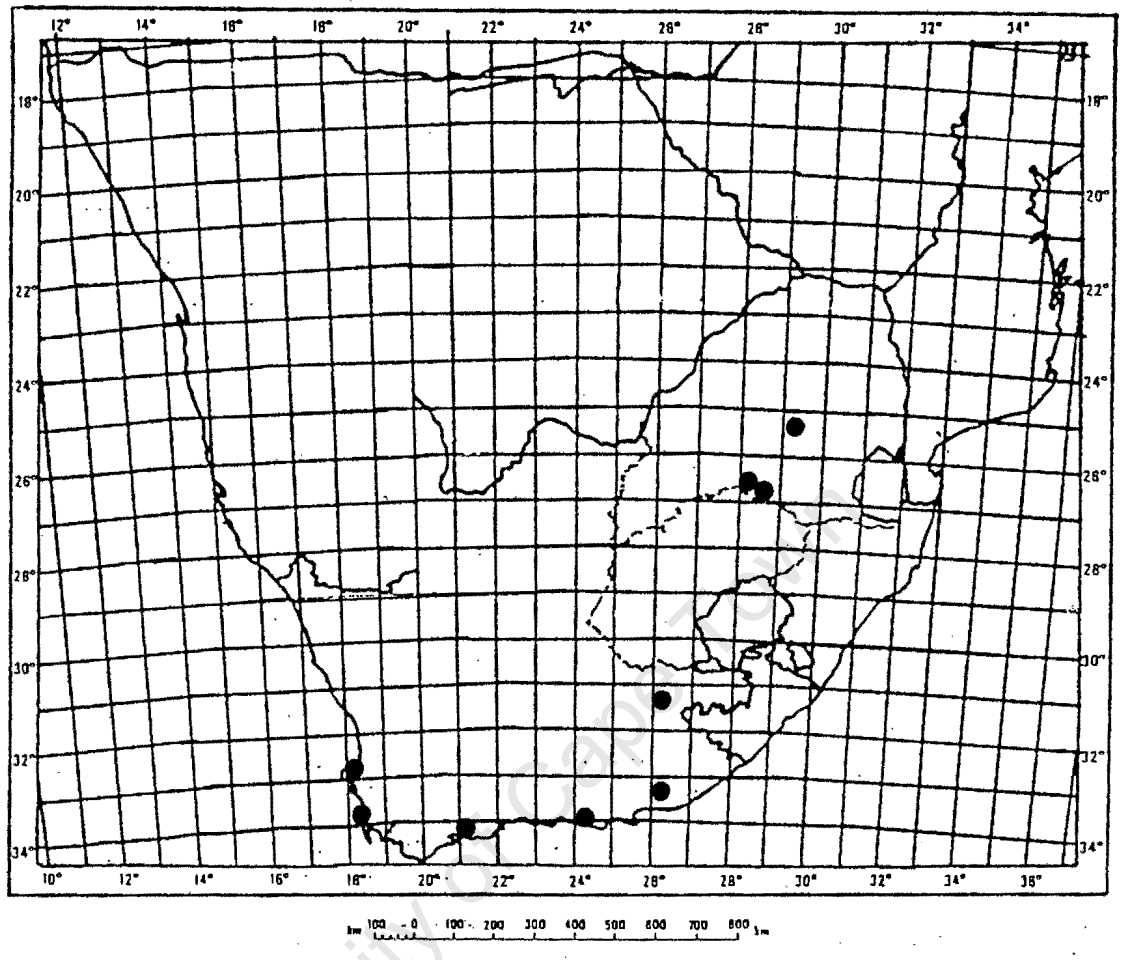


Fig. 12. Known geographical distribution of Avena sativa in southern Africa.

non-disarticulating spikelets at maturity.

Voucher specimens: Bolus s.n., (NBG); Esterhuysen 609, (NBG).

4. *Avena sterilis* L., Sp. Pl.: 118 (1753); Stapf in FC. 7:479 (1899); Hubbard, F.T.A.: 122 (1937); Grasses: 215 (1954); Clayton, F.T.E.A.: 84 (1970). Type: s.l. (holo. LINN - Microfiche BOL !).

Plants annual, single or several stemmed. **Culms** slightly robust or slender, erect, sometimes curved at base, 50 -- 145cm long; simple with approximately 3 - 4 nodes; surface ribbed or smooth, nitid; apical internode sometimes exposed. **Leaves** few, sheaths loosely rolled on culms, glabrous; leaf blades expanded, 15 -- 50cm long, 4 -- 13mm wide, glabrous, acute, soft tipped, margins scabrid; ligule scabrid below, lobed or shortly toothed, 3 -- 6mm long. **Inflorescence** open, spreading, ovate, 13 -- 34cm long, nodes 6 - 12, rachis glabrous or scabrid; branches alternate. **Pedicels** not obscured by the spikelets, sometimes recurved, scabrid, apex gradually thickened. **Spikelets** numerous, ovate - lanceolate, 2 -3 flowered, pale or bright green, 20 -- 46mm long. **Glumes** subequal, lanceolate, acuminate, glabrous, nitid, margins hyaline, 20 -- 46mm long, 10 -11 nerved. Callus densely bearded. **Rachilla** scaberulous, 1 -- 2.5mm long, disarticulating above glumes but not between florets at maturity. **Lemma** ovate - lanceolate, 17 -- 36mm long, toothed, teeth 1 -- 1.5mm long, proximal 2/3 with short rigid hairs, shorter than the glumes, hairy up to awn insertion, awned from the middle. **Awn** geniculate,

31 -- 85mm; column dark brown, pubescent. **Lodicule** fleshy at base, 1.2 -- 2mm long. **Palea** two keeled, ciliate on keels, slightly shorter than the lemma. Anthers 2.3 -- 3.8mm.

Leaf Anatomy

Leaf outline: expanded and flat, arms horizontal or slightly elevated, not keeled. **Ribs and furrows:** adaxial and abaxial ribs and furrows present between all vascular bundles; adaxial ribs more pronounced than the abaxial ones; ribs 16 - 18, big, slightly wide, forrows shallow, wide. **Median vascular bundle:** not structurally distinct from the lateral first order vascular bundles. **Vascular bundle arrangement:** vascular bundles vary in number, 8 or 9 first order vascular bundles and 7 or 9 second order vascular bundles between consecutive first order vascular bundles, third order vascular bundles absent, vascular bundles associated with the ribs, situated in the centre of the blade. **Vascular bundle structure:** first order vascular bundles almost rounded, slightly oval, second order vascular bundles round, with a distinct phloem and xylem, phloem not lignified, adjoining the inner vascular bundle sheath, metaxylem cells conspicuous, in groups of 5 or 6, more or less isodiametric. Vascular bundle sheath: double, outer bundle sheath composed of parenchyma cells, interrupted on the abaxial side, cells smaller than the mesophyll cells and lacking chloroplasts; mestome sheath cells smaller than the outer bundle sheath cells, not thickened. **Sclerenchyma:** Adaxial and abaxial sclerenchyma strands present, adjacent to the upper and lower epidermis respectively, not well developed; **Parenchyma girders:** present, sometimes continuous from the lower

to the upper epidermis, in rows of two or three, always associated with vascular bundles, abaxial parenchyma girders not always present. **Mesophyll:** irregular; intercellular spaces frequent, lateral cell count more than 4, continuous between bundles. **Adaxial epidermis:** cells not distinct from abaxial epidermal cells, not thickened, bulliform cells distinct, large, in groups of four or five, no macrohairs. **Abaxial epidermis:** structurally similar to abaxial epidermis, lacking bulliform cells and macrohairs. Cuticle absent.

Flowering time: September - November

Distribution, ecology and delimitation of species:

This weedy species of European origin is found in the Transvaal and the Cape (Fig. 13). Its habitats include waste places, disturbed areas where it grows on sandy soil.

Voucher specimens: Bolus 24908, (NBG).

5. *Aira* L., Sp. Pl.: 63 (1753); Stapf. in F.C. 7:463 (1899); Chippindall, Grasses and Pastures of South Africa: 86 (1955); Clayton, F.W.T.A.: (1972); Dyer, The Genera of southern African Flowering Plants 2: 833 (1976); Tutin in Fl. Europ. 227 (1980) Clayton and Renvoize, Genera Graminum: 131 (1986).

Genus description for the F.S.A. region as for species below.

There are eight species of this genus in the world, native in Europe and Mediterranean to Iran. Two species have been reported

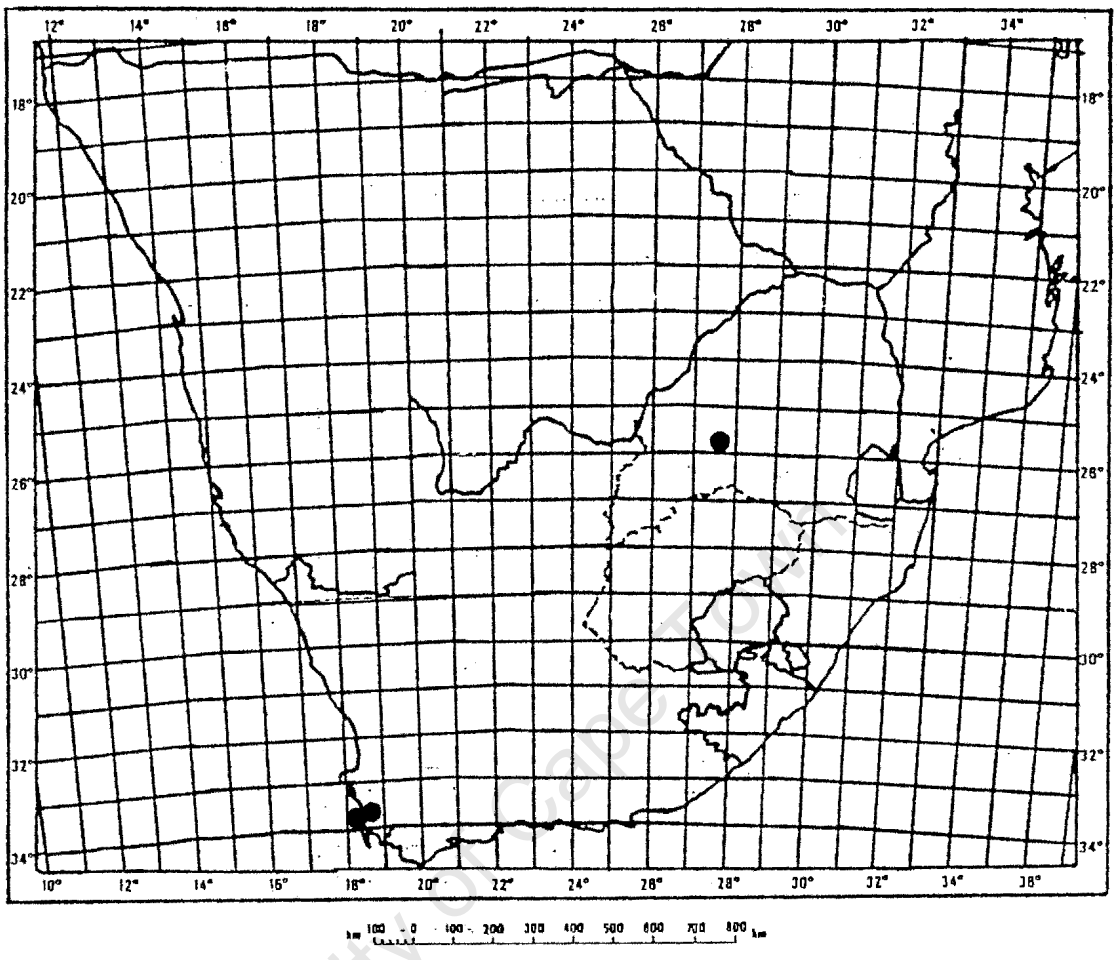


Fig. 13. Known geographical distribution of Avena sterilis in southern Africa.

to have been introduced in the F.S.A. region. These include *A. caryophyllea* and *A. cupaniana* Guss (Chippindall, 1955). This study reveals that it is difficult to distinguish between these two species as the characters on which they are delimited dubious. Clayton (1970) stated that the African material seems to intergrade and that it is difficult to separate the two species in Africa. Clayton (1970) applied the name *A. caryophyllea* to all the African material since it is the older name. Although this was based on material from the Flora of Tropical East Africa it seems as if it is equally true for material in the F.S.A. region. This treatment therefore, concurs with Clayton (1970). The generic treatment of *Aira* is limited to the F.S.A. material
See Fig. 14 for variation of some characters.

Aira caryophyllea L., Sp. Pl.: 66 (1753); Nees, Linnaea 7:306 (1831); Kunth., Enum. Pl. I: 289 (1833); Nees, Fl. Afr. Austr.: 272 (1841); Durand and Schintz, Consp. Fl. Afr. V: 834 (1895); Stapf in FC. 7:463 (1899); Lamson - Scribner, American Grasses 1:152 1900); Hubbard, F.T.A. 10: 87 (1937); Adamson in Adamson and Salter, Flora of the Cape Peninsula: 67 (1950); Hubbard, Grasses: 233 (1954); Chippindall, Grasses and Pastures of South Africa: 86 (1955); Martin & Noel, Albany and Bathurst Flora: 19 (1963); Clayton, F.T.E.A. 1:84 (1970); Ross, Fl. Natal: 89 (1972).

Note: The type specimen is listed in Savage's catalogue to the Linnaean herbarium but it is not in the microfiche collection.

A. latigluma Steud, Syn. Pl. Glum. 1:221 (1954); *A. latigluma* var. *latigluma* (Steud) C.E. Hubbard, F.T.A. 10:88

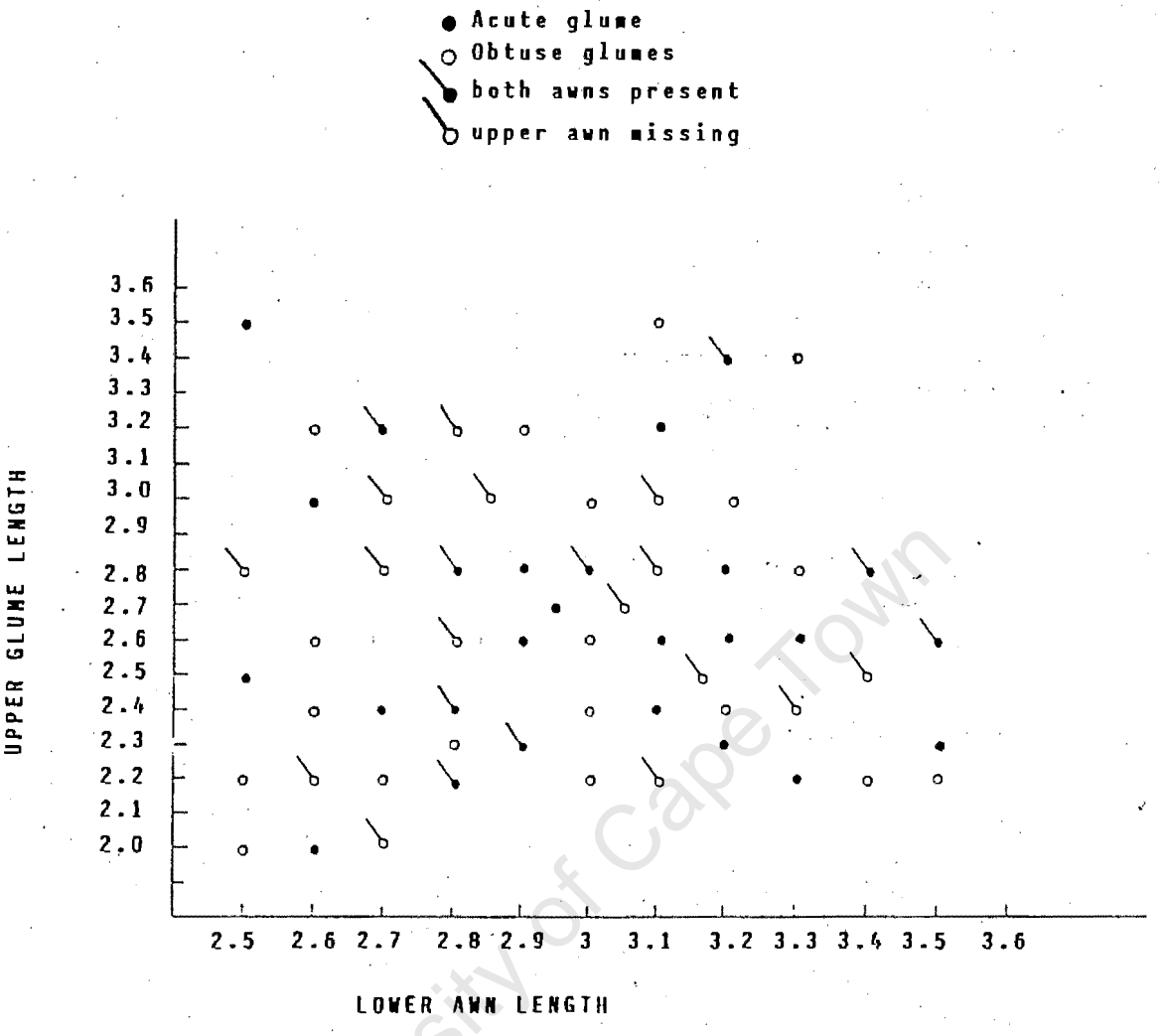


Fig. 14. Scatter diagram showing variation in Aira caryophyllea

(1937).

A. cupaniana Guss., Fl. Sic. Syn. 1:148 (1843); Hubbard, Grasses: 233 (1954); Chippindall, Grassesand Pastures of South Africa: 87 (1955); Clayton, F.T.E.A.: 86 (1970).

Plants annual, single or several stemmed. **Culms** slender, erect, sometimes geniculate, 3 -- 40cm tall; simple with approximately 5 - 8 nodes; surface ribbed, nitid; apical internode exposed. **Leaves** mostly basal; sheaths tightly rolled on culms, glabrous; leaf blades convolute, 1 -- 9.5cm long, up to 3mm wide, scaberulous on both surfaces, truncate, setaceous, margin scabrid; ligule membranous, glabrous with entire or dentitulate apex, 3 - 5mm long. **Inflorescence** ovate, sometimes oblong, 1 -- 14cm long; nodes 6 - 12, slightly swollen; rachis glabrous; branches filiform, in alternate pairs, terminal one sometimes unpaired. **Pedicels** erect, not obscured by spikelets, scabrid; apex gradually or abruptly thickened. **Spikelets** numerous, ovate, 2 -flowered, pale green, sometimes purple, clustered towards the branch tips, 2 -- 3mm long. **Glumes** subequal or equal, ovate, acuminate or subobtuse, glabrous, nitid, 2 -- 3mm long, 1 - nerved. **Callus** minutely bearded, lower sometimes less bearded than upper. **Rachilla** glabrous, up to 0.5mm long. **Lemmas** ovate, scabrid on upper half, 1.5 -- 2mm long, one quarter shorter than the glumes, acuminately bilobed, awned or lower one awnless. **Awns** geniculate, 2.5 -- 3mm long, arising from the lower one third, exserted beyond the glumes. **Lodicule** fleshy at base, 0.1 -- 0.3mm long. **Palea** two-keeled, scabrid, slightly shorter or equal to lemma. **Anthers** brown, 0.2 -- 0.4mm long.

Leaf Anatomy

Leaf outline: reduced v-shape, sometimes margins overlapping. **Ribs and furrows:** present between all vascular bundles, ribs 7,-9 medium furrows deep, narrow. No abaxial ribs and furrows. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** first order vascular bundles alternate with second order vascular bundles. Vascular bundles 7, round to oval, corresponding with the ribs, situated in the centre of the blade. Phloem distinct from xylem, slightly lignified, adjoining the inner vascular bundle sheath. Metaxylem cells conspicuous, in groups of 3 or 4. **Vascular bundle sheath:** double; outer bundle sheath composed of more or less isodiametric parenchyma cells, absent from abaxial side, cells smaller than the mesophyll cells and lacking chloroplasts. Mestome sheath cells smaller than the outer bundle sheath cells, inner radial tangential walls thickened. **Sclerenchyma:** abaxial sclerenchyma strands always present below vascular bundles adjacent to the epidermal cells and at margins, not well developed; no adaxial sclerenchyma strands or sometimes well developed below the median vascular bundle and at margins. **Parenchyma girders:** lacking. **Mesophyll:** irregular; tending to being radiate, cell shape irregular, intercellular spaces infrequent. Lateral cell count more than 4, continuous between bundles. **Adaxial epidermis:** cells smaller than abaxial epidermal cells. Bulliform cells distinct, large, in groups of four to five at bases of furrows, stomata present. **Abaxial epidermis:** stomata absent, sometimes arm cells present. Cuticle present, forms a

thin layer. Prickles present, few. Festucoid anatomy.

Flowering time: September - March

Distribution, Ecology and Delimitation of species:

This species occurs on the mountains of Natal Drakensberg to the south and south western Cape (Fig. 15). With its origin in Europe, *Aira caryophyllea* has become naturalised in the Fynbos and Grassland biomes. In these biomes it is common on shallow soils in damp to wet areas. In this study *A. caryophyllea* incorporates material which in Europe has been referred to as *A. cupaniana*. In the F.S.A. region these species cannot be separated from each other. In its native environments, *A. caryophyllea* is distinguished from *A. cupaniana* by having acute to acuminate glume apices and two awns while the latter has obtuse glume apices and one awn.

The distribution of these two species does not overlap in Europe. In the F.S.A. region all the plants referred to as *A. caryophyllea* are sympatric, and plants with one awn are usually found with plants with two awns. In some cases these two characters are found in one plant. Most of the plants in this genus have both character combinations in one plant, i.e. blunt glumes and almost acute glumes and also with either one or two awns. This has made it impossible to separate these species in the F.S.A. region. Adding to the problem is that the glume apex is very difficult to quantify as a character. This is more so when a decision must be made when this character falls somewhere between obtuse and acute. The cut off point from obtuse to acute

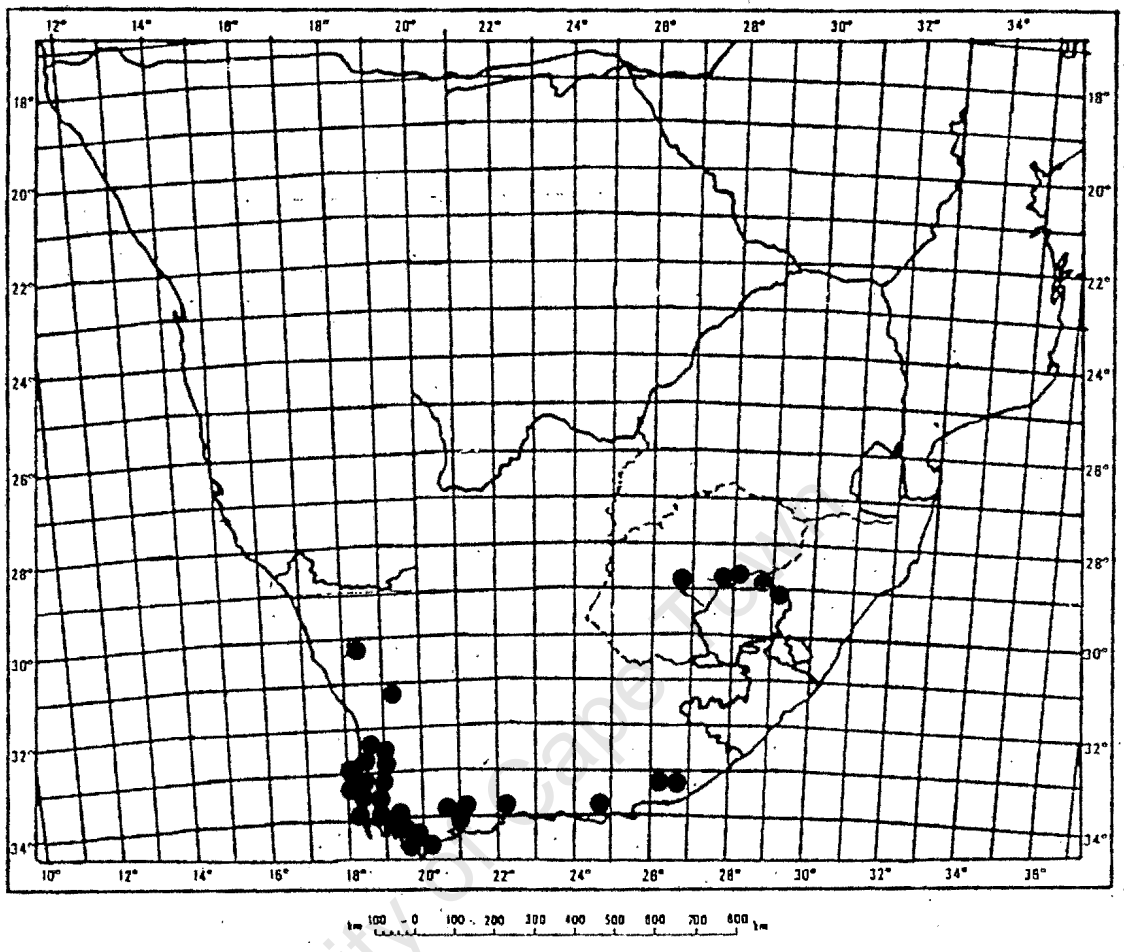


Fig. 15. Known geographical distribution of Aira caryophyllea in southern Africa.

becomes very subjective.

According to Chippindall (1955) *A. cupaniana* is distinguished from *A. caryophyllea* by blunter glumes and lemmas usually less than 3/4 the length of the glumes, the lower sometimes awnles. As these characters are variable they do not seem to justify the separation of these taxa. The only character that seems to be consistent is the absence of an awn in the lower lemma. Some specimens with blunter glumes also possess two awns, with lemmas 3/4 the length of glumes. (See Fig. 14)

Clayton (1970) commented that there seems to be some integration between the two species as far as the glume apex character is concerned. As a result of this he also included both species under one name, *A. caryophyllea*. Although I follow Clayton (1970) in using *A. caryophyllea* for South African material, *A. cupaniana* Guss cannot be treated as a synonym since only the South African material was seen.

Voucher specimens: Davidse 33862, (PRE); van Wyk 1973; (PRE); van Zyl 3477, (PRE); van der Walt, 243, (PRE).

6. *Arrhenatherum* Beauv., Ess. Agrost: 152 (1812); Chippindall, Grasses and Pastures of South Africa: 81 (1955); Dyer, The Genera of southern African Flowering Plants 2: 836 (1976); Holub in FL. Europ. 5:216 (1980); Clayton and Renvoize, Genera Graminum: 124 (1986).

A genus of six species, indigenous in Europe, Mediterranean and Middle East. Only one species in the F.S.A. region, cultivated in

Natal, escaped in the Cape. Thus the genus description for the F.S.A. region is as for the species. The genus *Arrhenatherum* is seperated from *Helictotrichon* only by its dimorphic florets otherwise they are morphologically similar.

Arrhenatherum elatius (L.) Beav. ex J. et C. Presl, Cechica, 17 (1819); Chippindall, Gr. & Past. S. A., 81 (1955); Lamson-Scibner, American Grasses, 1 (167) (1900).

Avena elatior L. Sp. Pl.: 79 (1753). Type: s.n. (holo. LINN - Microfiche, BOL.!). The type image in the microfiche collection of LINN is not clear as only the general external appearance of the specimen could be seen.

Plants perennial. **Culms** slightly robust, erect or curved at base, 50 -- 140cm long; simple with approximately 5 nodes,; surface ribbed, nitid; apical internode exposed. **Leaves** sometimes basal; sheaths loosely rolled, glabrous; leaf blade expanded, 10 -- 19cm long, 2 -- 5mm wide, puberulous or scaberulous above and below, acuminate, soft-tipped; margin scabrid; ligule membranous, glabrous with lobed apex, 1 -- 5mm long. **Inflorescence** open, sometimes dense and contracted, 8 -- 30cm long, narrowly oblong; rachis glabrous to scabrid; branches filiform, in whorls, conspicuously unequal. **Pedicels** not obscured by the spikelets, erect or recurved, puberulous, apex gradually thickened. **Spikelets** up to 60, ovate, oblong, 2-flowered, lower one male, upper bisexual, green with a tinge of purple, 7 -- 11mm long. **Glumes** unequal, lower oblong or lanceolate, 4 -- 5 mm long, upper ovate or lanceolate, acuminate, 5 -- 8mm long; both nitid,

glabrous, scabrid on keels, upper glume 3 nerved, lower 4 nerved. **Callus** bearded. **Rachilla** scaberulous to pubescent, 1 -- 1.5mm long. **Lemmas** oblong to lanceolate, puberulous up to awn insertion, 6 -- 8mm, acuminately bilobed, lower one awned from the lower third, awn 10-15mm, geniculate, upper one awned from the upper third or from the middle, awn 1 -- 3mm long. **Lodicules** fleshy at base, 1.9 -- 2.2mm long. **Palea** two keeled, ciliate on the margins, slightly shorter than the lemmas. **Anthers** brownish, 1.4 - 3.1mm long.

Leaf Anatomy

Leaf outline: expanded, flat, arms horizontal, keel well developed. **Ribs and furrows:** adaxial ribs and furrows present between all vascular bundles; ribs 28 - 30, big, slightly wide, furrows shallow, wide. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** first order vascular bundles alternate with second order vascular bundles, towards the margins first order vascular bundles replaced by second order vascular bundles, the latter replaced by third order vascular bundles. **Vascular bundle structure:** vascular bundles 26 - 29, round to oval, about the same size, associated with the ribs, situated in the centre of the blade. Phloem distinct from xylem, not lignified, adjoining the inner vascular bundle sheath. Metaxylem cells conspicuous, in groups of 5 or 6. **Vascular bundle sheath:** double, outer bundle sheath composed of more or less isodiametric parenchyma cells, interrupted on the abaxial side, cells smaller than the mesophyll cells lacking chloroplasts; mestome sheath cells smaller than the

outer bundle sheath cells, not thickened. **Sclerenchyma:** Abaxial sclerenchyma strands always present, adaxial sclerenchyma strands sometimes present, adjacent to the upper and lower epidermal cells respectively, not well developed except below the median vascular bundle. **Parenchyma girders:** present, sometimes continuous from the lower to the upper epidermal cells, in rows of two or three, always associated with vascular bundles. Abaxial parenchyma girders not always present. **Mesophyll:** irregular; cell shape irregular, intercellular spaces frequent. Lateral cell count more than 4,continuous between bundles. **Adaxial epidermis:** cells not distinct from abaxial epidermal cells. Bulliform cells distinct, large, in groups of four or five. Stomata present on both surfaces, infrequent on abaxial surface. Cuticle absent.

Flowering time: November - December

Distribution, ecology and delimitation of species:

Although it is a European grass, *A. elatius* has naturalised in the F.S.A. region where it was originally cultivated as pasture grass in Natal. It has subsequently escaped to the Cape (Fig. 16). It is frequently found in meadows, disturbed places, roadsides and also in gardens. It is characterised by its lower male floret with a geniculate dorsal awn and the upper bisexual floret with a short slender straight awn. Two forms of this species were seen, one form with bulbous, corm-like base, subsp. *bulbosum* (Willd.) and the typical one
lacks this characteristic, subsp. *elatius*.

Voucher specimens: Pent s.n., (PRE); Salter 9162, (BOL).

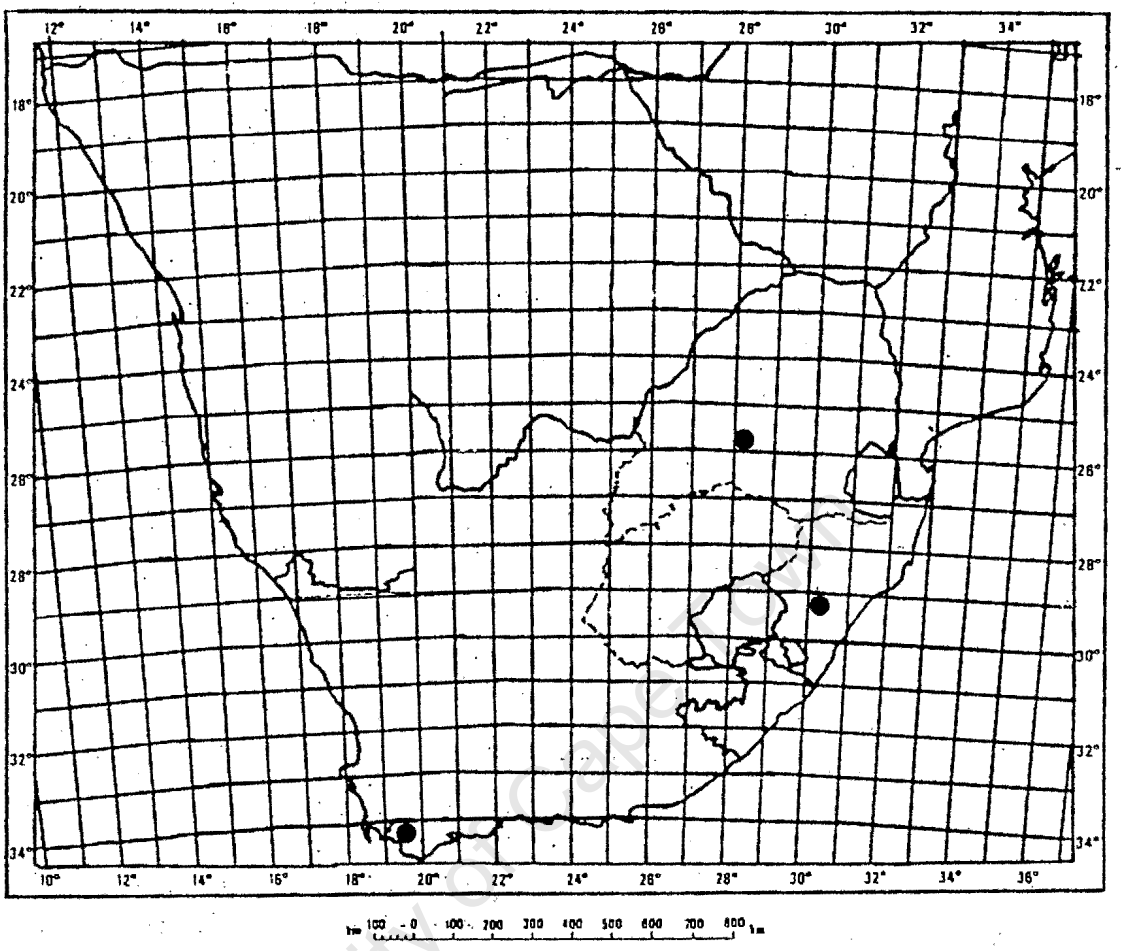


Fig. 16. Known geographical distribution of Arrhenatherum elatius in southern Africa.

7. *Koeleria* Pers., Syn. Pl.: 1:97 (1805); Stapf in F.C. 7:468 (1899); Stent in Bothalia 1:301 (1924); Adamson in Adamson and Salter, Flora of the Cape Peninsula: 84 (1950) p.p.; Chippindall, Grasses and Pastures of South Africa: 83 (1955); Clayton, F.T.E.A.: (1972); Launert in FZ. 10:69 (1971); Dyer, The Genera of southern African Flowering Plants 2: 866 (1976); Clayton and Renvoize, Genera Graminum: 127 (1986).

Koeleria is a genus of about thirty-five species distributed in temperate regions throughout the world. It is represented in the F.S.A. region by *K. capensis* The generic description for the F.S.A. region therefore is as for the species. It is closely similar to the genus *Lophochloa*.

Koeleria capensis (Steud.) Nees, Linnaea 7: 321 (1832); Kunth., Enum. Pl.: 382 (1833); Durand and Schinz, Consp. Fl. Afr. V: 892 (1895); Adamson in Adamson and Salter, Flora of the Cape Peninsula: 84 (1950); Chippindall, Grasses and Pastures of South Africa: 83 (1955). Clayton in F.T.E.A.: 79 (1970); Launert in F.Z., 10 (1): 69 (1971).

Aira capensis Steud in Flora II: 469 (1829). Type: Ecklon herb. s.n., (holo.).

K. cristata (L.) Pers., pro parte, Syn. Pl, I: 97 (1805); Kunth., Enum. Pl.: 383 (1833); Suppl.: 318 (1835); Durand and Schinz, Consp. Fl. Afr. V: 892 (1895); Phillips, Fl. Leribe: 343 (1917); Chippindall, Grasses and Pastures of South Africa: 83 (1955)

Festuca cristata L. Sp. Pl.: 76 (1753). Note: Linnaeus (1753) cites Loefling after the phrase name indicating that the name was based on his collection which is housed at LINN. This however is not in the microfiche collection of LINN.

Koeleria alopecurus Nees, Linnaea 7: 320 (1832); Type: Ecklon herb. s.n. (holo.); Kunth. Enum. Pl.: 383 (1833); Suppl.: 318 (1835); Durand and Schinz, Consp. Fl. Afr. V: 892 (1895); Adamson and Salter, Flora of the Cape Peninsula: 84 (1950);

NOTE: The type specimen of this species is probably amongst Nees' material acquired by B. in 1855. Nine thousand five hundred and fifty nine of these specimens are now destroyed, so it is possible that the type specimen has also been destroyed.

Plants perennial, densely caespitose, sometimes rhizomatous. **Culms** slender, erect or curved at base, sometimes bulbous at base, 15 -- 80cm long; simple with approximately 3 nodes; surface ribbed, nitid; apical internode sometimes exposed, hairy. **Leaves** mostly basal, sometimes inflated at base; sheaths tightly rolled, puberulous; leaf blades rolled to convolute or sometimes expanded, 4 -- 21cm long, up to 4mm wide, glabrous or scabrid, setaceous, pungent or soft-tipped, acute; ligule lobed, glabrous with ciliate at apex, 1 -- 2mm long. **Inflorescence** contracted, dense, continuous or interrupted towards the lowermost node, spiciform, 5 -- 14cm long, linear to lanceolate, nodes 5 - 12, rachis scabrid to pubescent; branches conspicuously short, in alternate clusters. **Pedicels** obscured by spikelets, scabrid, villous; apex gradually thickened. **Spikelets** numerous, oblong, 2

- 4 flowered, pale green, sometimes with a tinge of purple, nitid, 3.5 -- 4mm long. **Glumes** subequal or unequal, lanceolate - oblong, acuminate, acute, glabrous, scabrid or pubescent, lower 2.8 -- 3.2mm long, 1 nerved, upper 3.1 -- 4mm long, 3 nerved. **Callus** minutely bearded. **Rachilla** scabrid to puberulous, lower one missing, upper up to 1mm long. **Lemmas** elliptic - oblong, 3.5 -- 4mm long, upper one slightly longer than the glumes, acuminate, acute, rarely obtuse or mucronate. Lodicule fleshy at base, 0.6 -- 1mm long. **Palea** two keeled, glabrous, shorter or as long as the lemmas, projected from the lemmas and conspicuous at maturity. **Anthers** brown, 1.8 -- 2mm long.

Leaf Anatomy

Leaf outline: reduced v- or u-shaped, keel absent. **Adaxial ribs and furrows:** present between all vascular bundles, ribs 11 - 13, sometimes 5, big, slightly wide, furrows deep, narrow. No abaxial ribs and furrows. **Median vascular bundle:** not structurally distinct but bigger than the lateral vascular bundles. **Vascular bundle arrangement:** first order vascular bundles alternate with second order vascular bundles, towards the margins first order vascular bundles are replaced by second order vascular bundles, the latter replaced by third order vascular bundles. Vascular bundles 11 - 13, round to oval, about the same size, corresponding to the ribs, situated in the centre of the blade. Phloem distinct from xylem, not lignified, adjoining the inner vascular bundle sheath. -Metaxylem cells conspicuous, in groups of 4 or 5. **Vascular bundle sheath:** double; outer bundle sheath composed of more or less isodiametric parenchyma cells, absent on

the abaxial side, cells smaller than the mesophyll cells and lacking chloroplasts; mestome sheath cells smaller than the outer bundle sheath cells, sometimes radially thickened. **Sclerenchyma:** abaxial sclerenchyma strands always present, adjacent to the epidermal cells, adaxial sclerenchyma strands sometimes absent, when present very reduced and adjacent to the upper epidermal cells or sometimes well developed below the median vascular bundle. **Parenchyma girders:** sometimes present abaxially, otherwise lacking. **Mesophyll:** irregular; tending to being radiate, cell shape irregular, intercellular spaces infrequent. Lateral cell count more than 4, continuous between bundles. **Adaxial epidermis:** cells smaller than abaxial epidermal cells. Bulliform cells distinct, large, in groups of three at bases of furrows, stomata present. **Abaxial epidermis:** stomata lacking, cells bigger than adaxial epidermal cells. Cuticle present, forms a thin layer. Anatomy festucoid.

Flowering time: October - January

Distribution, ecology and delimitation of species:

K. capensis occurs mainly on the high mountains of eastern tropical Africa, southward to the Cape Peninsula. It is recorded in Uganda, Kenya, Tanzania, Zambia, Zimbabwe, Malawi, Mozambique, Transvaal, Swaziland, Natal, Lesotho, O.F.S., eastern and southern Cape (Adamson, 1950; Clayton, 1970). See Fig. 17 for F.S.A. distribution. It is not clear whether this species was introduced from elsewhere or its occurrence here is part of its cosmopolitan distribution. It is common in montane grasslands, sometimes among rocks and on steep slopes and dry to wet areas.

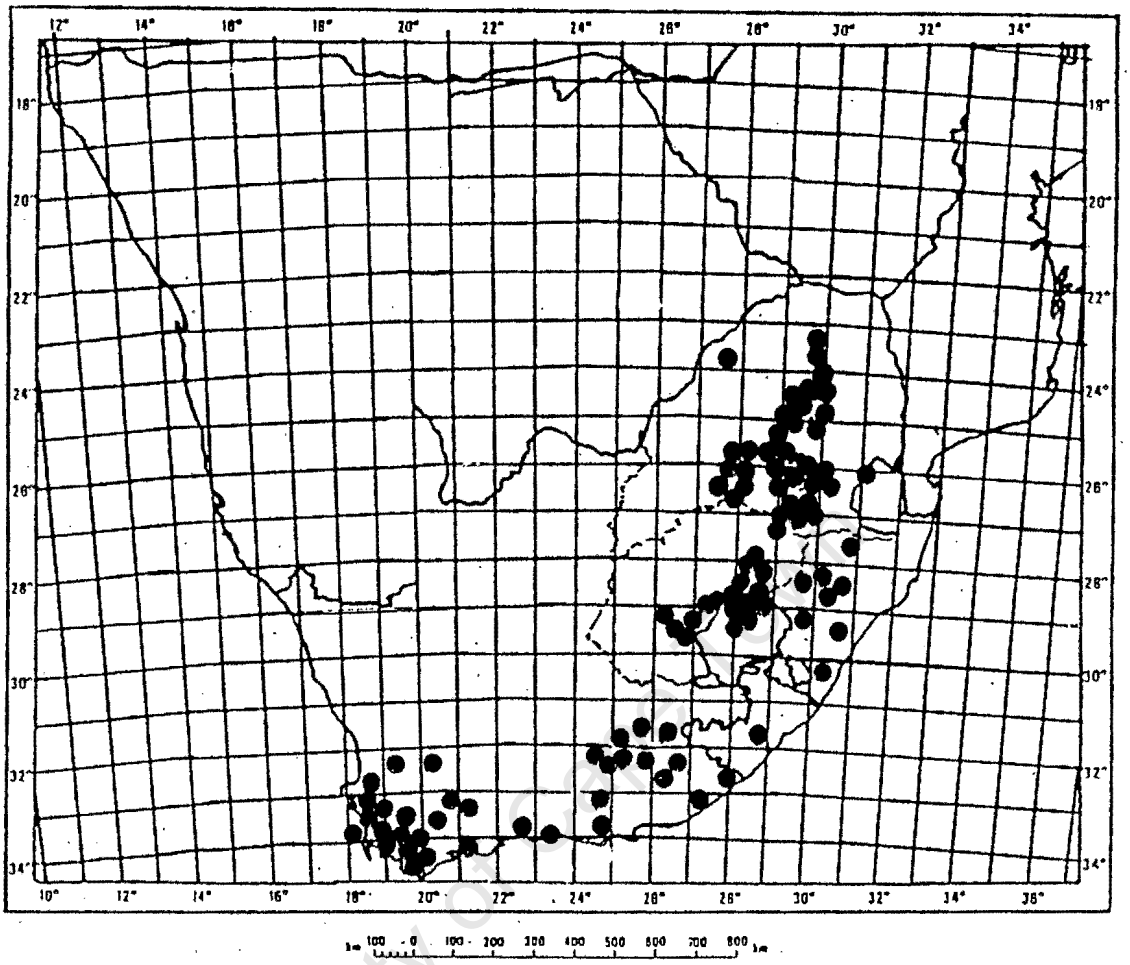


Fig. 17. Known geographical distribution of Koeleria capensis in southern Africa.

It is found in the Fynbos and Grassland biomes.

According to Clayton (1970) and Launert (1971) *K. capensis* is distinguished from *K. cristata* on the basis of the decaying soft, papery leaf sheaths found in the latter, whereas the former has hard decaying leaf sheaths. Based on this character, Adamson and Salter (1950) also recognised *K. capensis.* This is a subjective character and I have not been able to confirm the difference. *K. cristata* therefore is treated as synonym of *K. capensis* in this study.

Most plants of this species demonstrate vegetative proliferation towards the base of the inflorescence. This is a variable species especially in plant size, leaf indumentum and whether the leaves are flat, or rolled to convolute. However, it is easy to recognise due to its spiciform inflorescence, spikelets with 2 - 3 florets and mostly basal, slightly bulbous leaves, and slender culms.

A peculiar attribute of this species are the membranous paleas that stand out at maturity, gaping from their respective florets. This grass is used as a poor pasture grass since it is slightly palatable even in winter as it remains green for a longer period (Chippindall, 1955). In Lesotho it is used to weave hats and baskets, (Chippindall and Crook, 1976).

Voucher specimens: Behr 899, (PRE), Codd 3155, (PRE), Ebersohn s.n., (NBG).

8. *Periballia* Trin., Fund. Agrost.: 133 (1820); Chippindall,

Grasses and Pastures of South Africa: 86 (1955); Dyer, The Genera of southern African Flowering Plants 2: 833 (1976); Clayton and Renvoize, Genera Graminum: 131 (1986).

Molineria Parlatore, Fl. Ital. I: 236 (1850);

Molineriella Rouy., Fl. France 14: 102 (1913); Adamson in Adamson in Adamson and Salter, Flora of the Cape Peninsula: 67 (1950); Tutin in Fl. Europ. 5: 228 (1980);

This is a genus of three species from the Mediterranean. It is represented by one species in the F.S.A. region, where only two populations have been seen. The genus description for the F.S.A. region is as for the species below.

Periballia minuta (L.) Asch. & Graebn.; Chippindall, Grasses and Pastures of South Africa: 86 (1955).

Aira minuta L. Sp. Pl.: 64 (1753). Note: This name was probably based on Loefling's collection since Linnaeus (1753) cites him after the phrase name. The image of the type specimen is not in the microfiche collection of LINN nor cited by Savage (1945). It is difficult to say where the type element could be since Loefling's types are supposed to be at LINN.

Molineriella minuta (L.) Rouy, Adamson in Adamson and Salter, Fl. Cape Penin.: 67 (1950); Tutin, Fl. Europ. 5: (1980).

Plants annual, many stemmed. Culms slender, erect, 3 -- 14cm; simple with approximately 2 nodes; surface smooth, nitid; upper part of apical internode exposed. Leaves filiform, smooth;

sheaths tightly rolled; leaf blades filiform, 0.7 -- 3cm long, up to 1.5mm wide, glabrous to scabrid, acute, soft-tipped; ligule membranous, entire, smooth, ovate, continued as a hyaline margin, 1 -- 2mm long. **Inflorescence** open, slightly swollen at nodes, broadly ovate, 1.5 -- 4cm long, nodes 3-5, rachis glabrous; branches filiform, spreading, smooth. **Pedicels** not obscured by spikeletes, smooth, apex gradually thickened. **Spikelets** numerous, oblong to obovate, 2 - flowered, smooth, pale green to purplish, 1 -- 2mm long. **Glumes** subequal, smooth, ovate, subacute, 3/4 as long as lemmas, 1 -- 1.5mm long, 1-nerved. **Callus** minutely bearded. **Rachilla** glabrous, up to 0.5mm long. **Lemmas** narrowly ovate, 1.5 -- 2mm long, glabrous, obtuse or truncate, longer than lemmas, awnless. **Palea** smooth, not keeled, rounded at the back, slightly shorter than lemma. **Anthers** up 0.5mm long.

Flowering time: August - September

Distribution, Ecology and Delimitation of species:

This Iberian species is restricted to the Cape Peninsula (Fig. 18) where it is locally common in moist shallow soil over ironstone.

This species may be confused with *Aira caryophyllea*, but it can be distinguished by its fairly open panicle, glumes that are shorter than lemmas and by the absence of awns. There are few populations of this species in its restricted area in Cape Penninsula.

Vouchers: Salter 8766 (BOL); (SAM); Adamson 55318, (SAM).

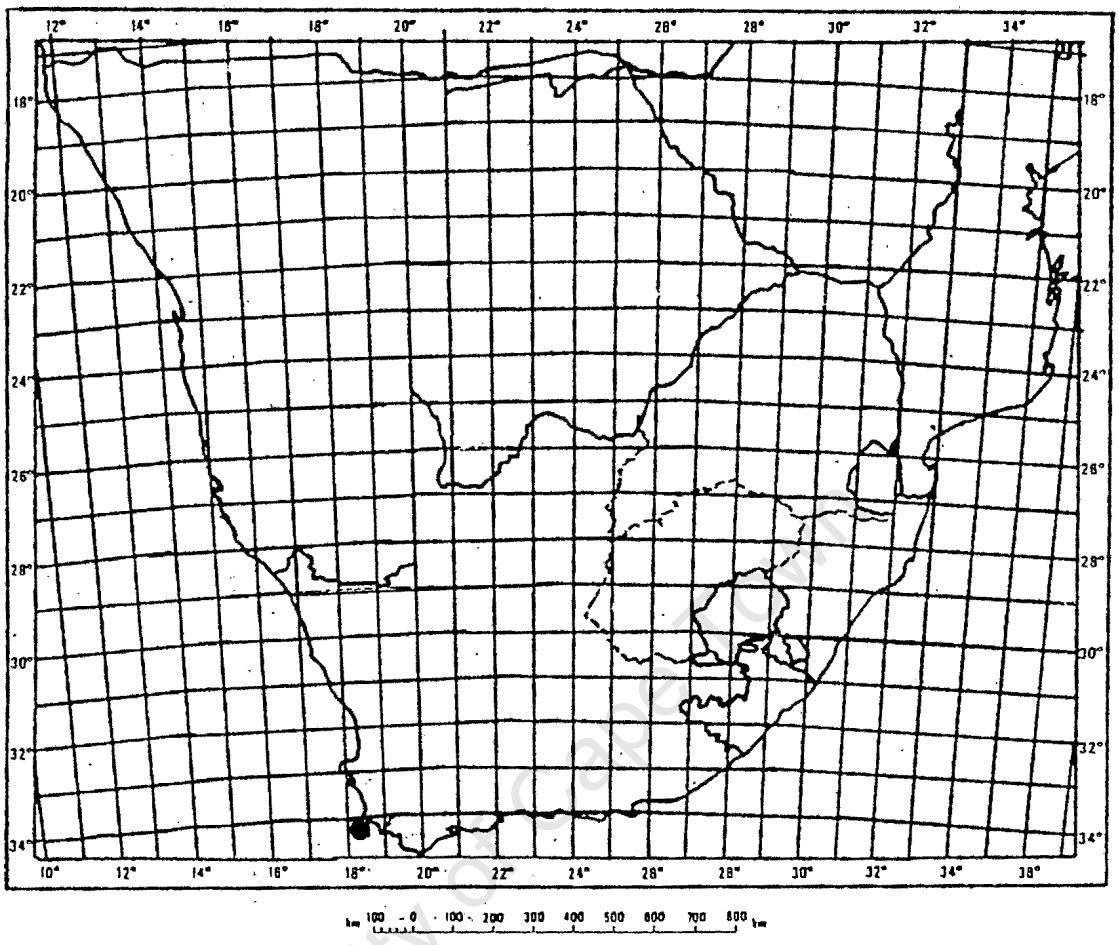


Fig. 18. Known geographical distribution of Periballia minuta in southern Africa.

2.1 Taxonomic value of Characters

It is difficult to identify any one set of characters that is reliable for identification at the generic level in the subtribe *Aveniae*. The reliable characters vary between genera. Certain characters, however, could be utilised in combination to succesfully delimit genera. The presence and absence of awns together with the awn length, when present, were used effectively to delimit genera. The number of florets proved to be an unreliable character since six of the eight genera studied share the same number of florets.

Below generic level a different set of characters becomes of taxonomic significance. Thus, there is no overlap between structures useful at the two levels. Plant size was not always useful at generic level although few genera could be distinguished on the basis of their size over and above other characters.

Members of this subtribe show a typical C3 anatomy. Their anatomy is non-krantz; the bundle sheath is always double with the cells of the inner bundle sheath smaller than those of the outer; lateral cell count between successive vascular bundles more than four. This group is also characterised by the presence of parenchyma girders and distinct bulliform cells in some of the genera (except *Koeleria, Lophochloa, Deschampsia* and *Aira).*

The anatomy of *L. pumila* could not be studied due to the unavailability of usable material. The anatomy of the genera with open, expanded leaves is relatively similar. They vary mainly in

the number of ribs and vascular bundles and the distribution of parenchyma girders. These characters seem to vary within species as well. In this study this group is represented by Fig. 19. The other group with u-shaped or reduced v-shaped leaf outline is represented by Fig. 20 and Fig. 21 respectively. This group demonstrates a Festucoid anatomy.

There is an apparent correlation between the habitats of the species and their anatomy, i.e. those species that are found in relatively moist areas have an open leaf outline and those that are found in dry areas and in high altitude areas have a reduced to a rounded leaf outline. A more indepth study needs to be be done so that the differences can be quantified.

Anatomical characters show considerable uniformity between species in the genus *Avena*. It is doubtful that taxonomic congruence would be obtained between morphological and anatomical characters if separate classifications were drawn up for this genus. Further investigation needs to be done in this regard. It is easy to distinguish between the other genera as their anatomical characters tend to be consistent within species.

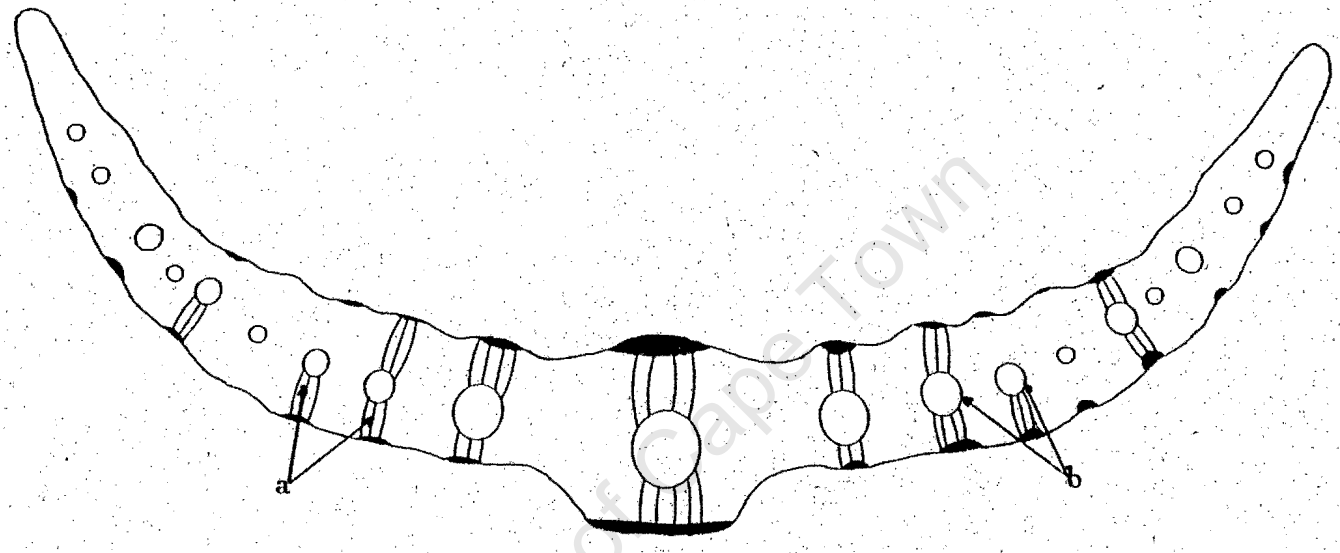


Fig. 19. Camera lucida drawing showing leaf cross section of Avena barbata, X150. Voucher: du Toit 476 (PRE).
a) Parenchyma girders
b) Vascular bundles
Shaded areas = Sclerenchyma

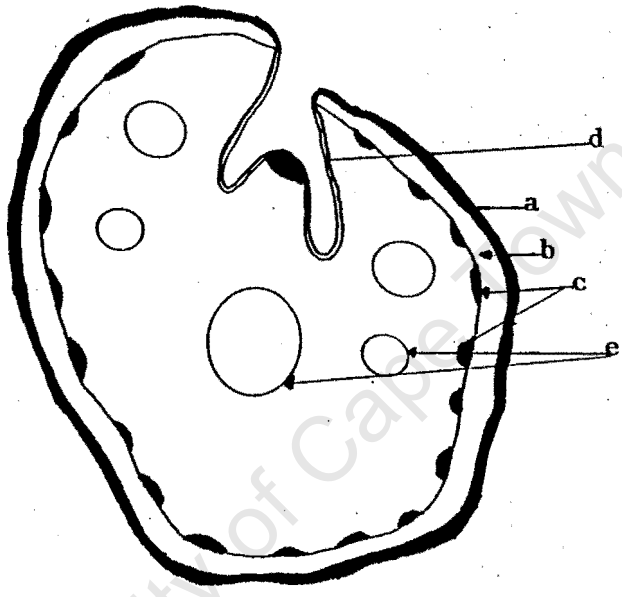


Fig. 20. Camera lucida drawing showing leaf cross section of Deschampsia flexuosa, X150. Voucher: Smook 524 (PRE).
a) Outer most shaded layer ≙ cuticle
b) Layer of abaxial epidermis
c) Sclerenchyma strands
d) Layer of adaxial epidermis
e) Vascular bundles

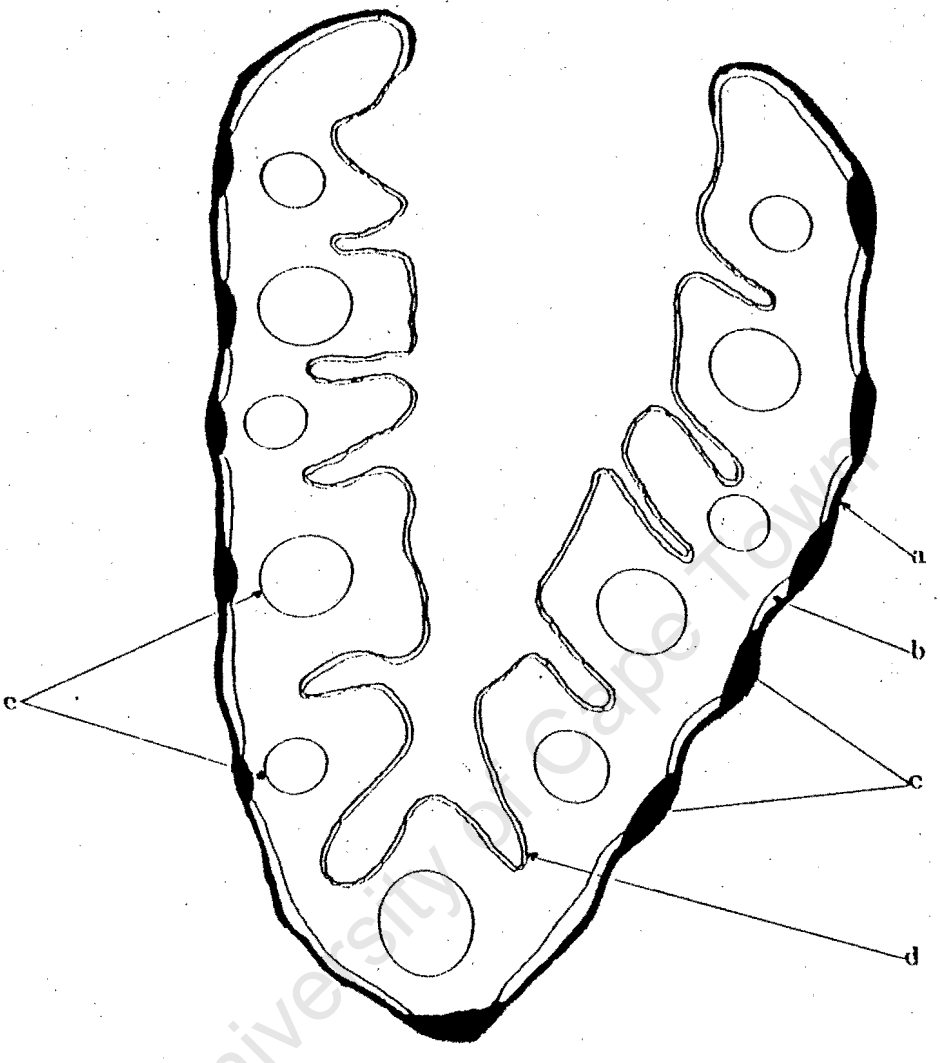


Fig. 21. Camera lucida drawing showing leaf cross section of Koeleria capensis, X150. Voucher: Cain 382 (NBG).
a) Outer most shaded layer = cuticle
b) Layer of abaxial epidermis
c) Sclerenchyma strands
d) Layer of adaxial epidermis
e) Vascular bundles

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SYSTEMATIC STUDIES IN THE GENUS *FESTUCA* L. (POACEAE)

I. THE VARIATION PATTERNS IN *FESTUCA CAPRINA* NEES.

II. A NEW SPECIES IN THE GENUS *FESTUCA* L.

PART 2

I. THE VARIATION PATTERNS IN *FESTUCA CAPRINA* NEES

II. A NEW SPECIES IN THE GENUS *FESTUCA* L.

I. THE VARIATION PATTERNS IN *FESTUCA CAPRINA* NEES.

TABLE OF CONTENTS

ABSTRACT

Festuca caprina Nees, is probably the most variable fescue in South Africa. The aim of this study is to clarify its taxonomic status and to determine its internal variation patterns.

Morphological, anatomical and cytological studies were made. Some of the morphology and anatomy data were treated by statistical pattern-seeking techniques. These included correspondence analysis and phenetic clustering. The variation patterns found by these techniques do not correlate with environmental differences.

The results also show that there is no correlation between morphological and anatomical character variations. The anatomical characters seem to vary at random. The two varieties of this species have been sunk to form a single variable species.

ACKNOWLEDGEMENTS

This project was done while holding a Foundation for Research Development studentship at the University of Cape Town. I am grateful to my supervisor, Dr. H. P. Linder for his guidence during the course of this study. I thank the staff of the systematics laboratory at the University of Cape Town, Miss J. Thompson and Miss P. Chesselet for their encouragement and advice. I gratefully acknowledge Miss B. Laurens for doing the morphological illustrations.

I also thank the members of staff of the Botany department, U.C.T. for their assistance at times when their help was most needed, especially Karen Wienand, who did the soil analysis and Drs. W. Stock and W. Bond for their advice.

I am indebted to Prof. A.V. Hall of the University of Cape Town who was responsible for supervising the final draft of this thesis.

My thanks are also due to Dr. R.P. Ellis of the National Botanical Institute for his patience and anatomical expertise. His standardised terminology is used in this thesis. I also thank Dr. R. Knight of the University of Transkei for critically proof reading this thesis. Any mistakes are my own.

I also thank my wife, Nosisi, for her support, encouragement and love throughout this project and also for proof reading this thesis.

To my mother, without whom I would have not been able to reach this level of my studies, I dedicate this dissertation.

CHAPTER 1: Introduction

The genus *Festuca* L. is a relatively large genus of about 450 species, (Clayton and Renvoize, 1986) with a cosmopolitan distribution, (Dahlgren et al., 1985; Clayton and Renvoize, 1986). It is extensively distributed in temperate regions at high altitudes (Clayton and Renvoize, 1986) with a concentration of species in Europe (Borril, 1972). Ten of these species occur in South Africa (Linder, 1986), including a species described for the first time in this thesis. This study will only concentrate on one of the South African species, *Festuca caprina* Nees.

Festuca caprina is a perennial, caespitose, several stemmed or sometimes single stemmed grass. This species is distinguished from other South African species of *Festuca* by its filiform and permanently folded leaves. Populations of *F. caprina* occur in mountain grasslands. Its distribution ranges from the eastern Cape on the Katberg and Sneeuberg northwards to the Kitulo plateau in southern Tanzania, occurring in between in Lesotho, through the Drakensberg grassveld in Natal to the eastern Transvaal, and Swaziland.

Festuca caprina is a good pasture grass (Bews, 1929). It is therefore possible that it does not occur naturally throughout its distribution range as it might have been locally introduced as pasture grass.

In the Drakensberg, this fescue is represented by several morphological variants which form distinct populations. This species is probably the most variable among the southern African fescues.

The characters that vary are: the degree of openness of the inflorescence, hairiness on lemmas, culm length, leaf length and tussock diameter.

There are three infra-specific taxa presently recognised in this species (Stapf, 1900; Clayton, 1970; Chippindall, 1955). The boundaries of these taxa are not clearly defined and the variation patterns are poorly understood. The characters on which the present taxa are delimited are seemingly variable, rendering their identity dubious. Recent attempts by Linder (unpubl.) to delimit these taxa on gross morphology have failed.

The South African species of *Festuca* do not seem to be closely related to each other, but have affinities with groups of species from other parts of the world (Kennedy-O'Byrne, 1963). *F. caprina* is characteristically closely related to *Festuca humidicola* Sokutu, a new species described in this study and also with *F. ovina* L. from Europe (Kennedy-O'Byrne, 1963).

The aim of this study is to clarify the taxonomic position of *Festuca caprina* and its infra-taxa and also to determine the pattern of population variation, in order to understand the relationships between and within the populations. This study represents a first attempt to characterise the variation of this species with regards to macro- and micro-morphology, anatomy and cytology. Other characters which may help to clarify the infra-specific variation in this species are reported.

It is hypothesised that *F. caprina* is a generalist species with each morphotype representing a distinct genetic specialisation.

This hypothesis is based mainly on field observations and on previous studies (Brown et al, 1978; Ringius & Chmielewski, 1987; Harnett et al, 1987, Snaydon & Davies, 1982) which will be described later in this thesis.

Gross plant morphology is an integral component of plant taxonomy and systematics. The recognition of different plant species according to their morphological attributes testifies to this fact. It can be argued therefore that morphological differences reflect, to a certain degree the differences in plant genotypes. Grasses are probably the most ecologically successful angiosperm group and one of the most morphologically complex groups (Bews, 1929). The most extensive classification of grasses in the last century is probably provided by Haeckel (1882) in Dahlgren et al. (1985). This classification was based primarily on morphological characters. This emphasis on morphological characters was questioned by Avdulov (1931) in Dahlgren et al (1985), who on the basis of cytology radically altered the classification. The new classification was supported by leaf anatomical characters and seedling morphology studied by Prat (1931) in Dahlgren et al, (1985). Since then anatomical characters have been very important in classification of grass subfamilies (Reeder, 1957; Ellis, 1986, 1987, 1988). Other characters have been incorporated and played an important role in the classification of grasses e.g cytology and embryology (Newell and De Wet, 1974; Dahlgren et al, 1985; Spies and Du Plessis, 1986-1988; Bassappa et al, 1987). However, morphological characters were still used for general classification purposes and identification such as for field work.

Ovary and caryopsis data do not have much value for separating taxa below species level. However, they can be useful at the generic (Chippindall, 1955; Barker, 1986) and specific levels (Ellis, 1985b; 1985c). The characters that are normally used include caryopsis shape, coat sculpturing and presence or absence of hairs on the stylar end of the caryopsis (Barker, 1986). These characters do not seem to be significant for distinguishing taxa below the species level. Therefore they will not be employed in this study.

Morphological characters, especially of the spikelet, do not only aid in recognising groups but also in understanding affinities between and within the different groups (Shaw and Smeins, 1979; Brown et al, 1978; Brody, 1983; Gibbs Russell and Ellis, 1988). Variation patterns can differ within and between generic, specific and infra-specific levels (Brody, 1983; Giles and Lefkovitch, 1986). Variation in morphological characters at the specific and below the specific level have been documented by several workers, e.g. (Baum, 1987; Dube and Morriset, 1987; Baum and Bailey, 1988; Scheiner and Teeri, 1987; Davidse, 1988). In this regard reproductive characters have proved to be reliable due to their conservatism. However Dubcosky and Martinez (1987) stated that reproductive and vegetative characters should be used jointly for general systematic purpose. However, this is not a general taxonomic principle as the use of characters is relative to the group being studied. Characters that are used in one group of plants need not be used in another group (Dewald et al, 1987; Lawrence, 1951). Although the spikelet and vegetative characters can be

used effectively to study variation patterns below specific levels, Dube and Morriset (1986) and Aiken et al (1985) have argued that the evidence can be used more convincingly when used in conjunction with evidence from other sources e.g. anatomical characters, etc. This is especially so if taxonomic/systematic congruence is obtained. Morphological characters have also been used jointly with cytological characters (Borill, 1972; Frederiksen, 1977; 1984; Dube and Morriset, 1987). The cytological characters have played an important role mostly in confirming taxa that can be distinguished morphologically (Dube & Morriset 1986). Variation of vegetative characters at infra-specific levels has also given insight to the causes of the resultant pattern. For example, if there is a correlation between the variable characters and the corresponding habitats in which the respective populations occur, it can be concluded that the differences reflect habitat differences either phenotypically or genotypically (Borill, 1972; Harberd and Owen, 1969; Dube and Morriset, 1987; Gibbs Russell and Spies, 1988; Taylor and Aarsen, 1988). In this study the morphological characters will be used in conjunction with cytology, anatomy and soil characteristics.

Gross morphology can also be used to clarify controversies around taxonomical positions of taxa i.e to lump or to split (Pavlick and Looman, 1984). External morphology can also be used below species level to test compatibility and incompatibility in making taxonomical decisions (Harberd, 1962).

It has been shown that patterns of phenotypic variation in both anatomical and morphological characters are equally affected by

the environment (Dube and Morriset, 1986; Davis, 1983; 1988; Dubcosky and Martinez, 1987, Ellis, 1988). Thus anatomical characters, at least below species level are generally not more or less affected by the environment as compared to morphological characters.

1.2. An Overview of Population Variation

Since the description of speciation by natural selection by Darwin (1859), many studies have been devoted to population variation. Population variation is most likely to occur where there is variation in spatial environmental conditions through time and space if the selection differentials are sufficiently large (Snaydon & Davies, 1971). Thus population variation is a function of survival of plant species, at the same time a function of evolution by accumulating small genetic changes through time (Stebbins, 1950). Morphological differentiation in different populations may be induced by climatic factors, edaphic factors and biotic factors. Thus, population variation can be defined as a means of adapting species to the changing environments (Ford,1973).

Population variability includes three components: developmental variability; phenotypic plasticity and genetic variability (Briggs and Walters, 1984). In developmental variability, adult plants are strikingly different from their seedlings, e.g. *Acacia* species. This difference is genetically based (Molgaard,1986). Environmental variability is due to the influence of the environmental factors e.g. light, precipitation, temperature, etc.

(Kjellqvist, 1961). Finally, in terms of genetic variability, gene flow and genetic recombination between individuals, populations, and species is mostly responsible for exchange of genetic information which in turn results in diversity among individuals (Ehrlich and Raven, 1977).

Populations may vary in their phenotypic expressions from habitat to habitat as conditions dictate or by changes in their genetic constitution. Thus a species can exist in a heterogeneous environment either if its populations are phenotypically flexible or if there is genetic variation among individuals, within or between populations (Jain and Rai, 1974). Phenotypic plasticity may therefore be defined as the ability for an organism to grow and reproduce in a range of habitats either by changes in its phenotype or by maintaining a constant phenotype (Scheiner & Goodnight, 1983), while changing aspects of their physiology (Amory, A.M. pers. comm.). However phenotypic plasticity occurs within a certain environmental range as it is under genotypic control, therefore subject to selective pressures (Briggs and Walters, 1984) . A number of studies have demonstrated that when phenotypic plasticity has reached its limit, individual plants vary in their genetic constitution, leading to a distinct population (Jain & Bradshaw, 1966; Thoday & Baum, 1959, Mcneily, 1968, Endler, 1986). This leads to the evolution of ecotypes.

Turesson (1922-1930) conducted a series of experiments to show that if representatives of species from different habitats are grown together in an experimental garden, they and their offspring preserve distinctive characteristics. It was therefore

concluded that these characteristics are genetically transferred through hereditary mechanisms. However there is also evidence that organisms may change in their phenotype while the genetic constitution remains constant. When the environment follows a gradient, observable gradual genetic changes are developed (McNeilly, 1968). This variation pattern is referred to as a clinal variation following an ecocline.

In their reciprocal transplants, Clausen et al (1939), isolated those changes induced by the environment from those inherent in the organisms themselves. These two sets of experiments allow discrimination between phenotypic plasticity and genotypic response. Turesson (1925) referred to populations adapted to their different habitats as constituting genotypic response. These adaptive races (Dobzhansky, 1951) are called ecotypes (Turesson, 1925). This means that whenever there are two or more habitats in the same or different geographic areas with the same environmental characteristics, the same ecotypes should occur in all of these habitats. Dobzhansky (1951), showed that in *Drosophila* some strains compete better than others at certain temperatures which correspond with their native habitats. It can be concluded therefore that ecotypes are the result of adaptation to the different prevailing habitats in a distribution range. Habitats may differ on a macro- or micro- geographical scale. As a result, ecotypes may occur on both of these scales. Where there are discontinuities in the environment, the ecotypes may exist as distinct populations in different habitats (Conrad and Clifford, 1987). However, when there is a gradual change in the environmental conditions, the two extreme races may be con-

nected by a series of intermediates (Dobzhansky, 1951) making it difficult to delimit them. This clinal pattern corresponds to gradual variation in environmental conditions respectively (Scheiner and Teeri, 1987). A study of the population structure in *Avena fatua* suggests that the isolated small subdivisions of populations are due to random genetic drift towards a highly varied pattern of differentiation, (Jain & Rai, 1974).

Another form of population variation may be due to the action of intense divergent selective pressures. This is also a genotypic variation. It is essentially the same as the variation of ecotypes except that it usually occurs on a micro- geographical scale. In this type of variation two or more populations of the same species may co-occur in the same area which may be subdivided by certain environmental factors. The different environmental factors induce genetic differences between the populations concerned. Dobzhansky (1951) showed that when *Drosophila* species are subject to a intense selective pressure their genetic constitution changes in such a way that only those populations of certain genotypic constitution survive in these environments. Under low selection pressure there was no population divergence. Thus population differentiation is most likely to occur where there is variation in environmental factors, stability in time, and space if the selection factors are sufficient. When populations are exposed to a mosaic environment, complex significant variation between them results (Snaydon & Davies, 1971). This is a response to the action of natural selection acting on genetic variation. The morphological differences would then be adaptive.

Adaptation to a heterogeneous environment may be achieved in several ways. One way is to maintain genetic polymorphism. Even under high rates of pollen dispersal (60%) between adjacent populations, divergence resulted due to intense disruptive selective force (Jain and Bradshaw, 1966). For example, when populations are edaphically restricted they are characterised by less genetic variation, in contrast to other populations which are not edaphically restricted (Antonovics and Bradshaw, 1970). These studies and many others e.g. McNeiley and Antonovics (1968); Thoday & Gibson (1962); Scheiner & Teeri (1987) show that populations may respond to changes in the environment by becoming genetically adapted even within a short period of six years.

There are a number of studies which show population genetic variation due to disruptive selection (Brown & Nevo, 1978; Ringius & Chmielewski, 1986; Harnett et al, 1987, Snaydon & Davies, 1982). Gene flow between adjacent populations does not seem to affect population divergence. Jain and Bradshaw (1965) argue that geographical discontinuity of species distribution is a prerequisite for the occurrence of any marked local differentiation, since any interchange of genes through pollen or seed dispersal is likely to counter balance the divergent local pressures that might be operating in various neighbourhoods.

Experimental evidence from studies presented above from several species of plants suggests that within a continuous range, distances separating contrasting populations may range from as short as less than 100m to less than 5m, distances over which gene flow can easily occur. Population differentiation therefore may depend

upon the amount of gene flow in combination with the magnitude of selection.

These studies indicate that under very intense selective pressures, gene flow, irrespective of the magnitude, does not affect population differentiation. On the other hand, under low selection pressures, high amounts of gene flow may prevent population differentiation; similarly under low selective pressures, low gene flow may not prevent population differentiation, (McNeiley, 1968). This is because population differentiation takes place over a long period of time during which the environment filters out poorly adapted genotypes.

In all the cases presented above whether phenotypic plasticity, genetic variation under different environmental conditions, or under different selective intensities- the species populations are becoming adapted to their respective habitats. This is the core of natural selection. Darwin's principle of natural selection states that if a population consists of different genotypes, some of them are likely to produce more surviving progeny than others. This principle has been criticised in the past on the basis that it assumes the presence of hereditary variation in population. This argument persisted until the discovery of Mendel's law and later the occurrence of mutations in natural populations by De Vries (1936) in Dobzansky (1951).

Mutations are the origin of variations in natural populations. These variations become transferred from one generation to another. This is the level where natural selection takes place (Dob-

zhansky, 1951). Those genotypes that are better adapted to their environments tend to be selected and therefore survive longer.

Breeding systems affect population variation in a number of ways. Out-breeding populations tend to maintain more genetic variation than in-breeding populations. This is due to the effect of new gene recombinations from existing genes. The differentiation of localised populations can be dependent on the interplay between natural selection, the breeding systems and gene flow (Jain and Bradshaw, 1966). Inbreeding populations transmit the same genotype from one generation to the next. The same may be said of asexual reproduction by vegetative parts e.g. rhizome, stolons, runners etc. The most important source of variability in nature is due to gene flow and recombinations between individuals, populations and species.

CHAPTER 2: Taxonomic History

The first scientific description of *Festuca caprina* was by Nees (1841), who recognised two varieties: var. *caprina* Nees and var. *curvula* Nees. Nees based his nomenclature and classification name on a Type specimen collected from Katberg in Queenstown district by Drege. 'Caprina' is Latin for goat-like. It is therefore possible that Drege learnt of the local common name through personal communication with the inhabitants of the area from which it was collected, and passed this information on to Nees. Alternatively Nees himself might have recognised the resemblance of the leaves to the goat's beard and suggested the name 'capri-na'.

Like many early taxonomists, Nees relied on macro-morphological characters in his treatment of this species. He used characters including size, habit and colour of spikelets at maturity. Some, if not all of these characters exhibit considerable phenotypic plasticity (Dobzansky, 1951). It appears that according to Nees any different morphotype represented a distinct variety or race. Subsequent to his description Stapf (1899) recognised two varie-ties, different from those of Nees (viz): var. *irrasa* Stapf and var. *macra* Stapf. Stapf's var. *irrasa* is distinguished by having hairy lemmas and var. *macra* by having rigid leaf blades which are scabrid on both surfaces and also longer awned lemmas.

In 1927 St. Yves included *F. caprina* as a subspecies of *F. nubigena* Jungh. (Clayton, 1970). Following the re-appraisal of this taxon to a specific rank this name was subsequently reduced

to a synonym of *F. caprina*. Chippindall (1955) followed Stapf in her treatment of this species. Other researchers including Kennedy O'Byrne (1963), Clayton (1970), Launert (1971), Compton (1976) and Ross (1973) referred to *F. caprina* as a single polymorphic taxon. These botanists however did not conduct any critical study of this species. Some of them commented that there are overlaps between the infra-specific taxa, making the distinction meaningless (Launert, 1971; Ross, 1973). However, no alternative key was suggested. Linder (Unpubl.) noted the apparent continuity in the characters used to distinguish between the various infra-specific taxa.

In his description of *F. caprina*, Clayton, (1970) notes that this species can be distinguished by its open panicle. From this comment it is obvious that he did not see other specimens with more closed panicles. However as he was working with material from East Africa, this may mean that all specimens of *F. caprina* from East Africa have open panicles.

CHAPTER 3: MATERIALS AND METHODS

3.1. STUDY AREA AND SAMPLING DESIGN

It was necessary to cover as wide a distribution range as possible so as to have a representative sample of study material. Thus, most of the known distribution range of this species in southern Africa was covered and collections were made at most of the localities. Voucher specimens were prepared and deposited in the Bolus herbarium (BOL). The South African populations are restricted to mountainous areas and the entire southern African variation is found in the Drakensberg. This region extends from the southern Drakensberg in Natal to the north eastern side in the Orange Free State.

Twelve populations were sampled, with four populations from Naude's Nek 3028CA (N1S, N2S, N1B, N2B); three from Sani Pass 2929CB (ST1, ST2, SS); two from Cathedral Peak (CP, AP); two from Wietzieshoek 2828DB (WH1, WH2) and one from Wodehouse Peak 2828CB (WDP) in the Golden Gate, (see table 1 for region codes and Fig. 1a for sampling sites). Within this area there is a large degree of population variation.

The study area was divided into five regions. The different regions do not necessarily represent different climatic conditions. They are geographical regions.

Population samples averaged about 25 individuals collected from the whole area occupied by the population. The sample size ranges from 10 to 30 individuals depending on the population size.

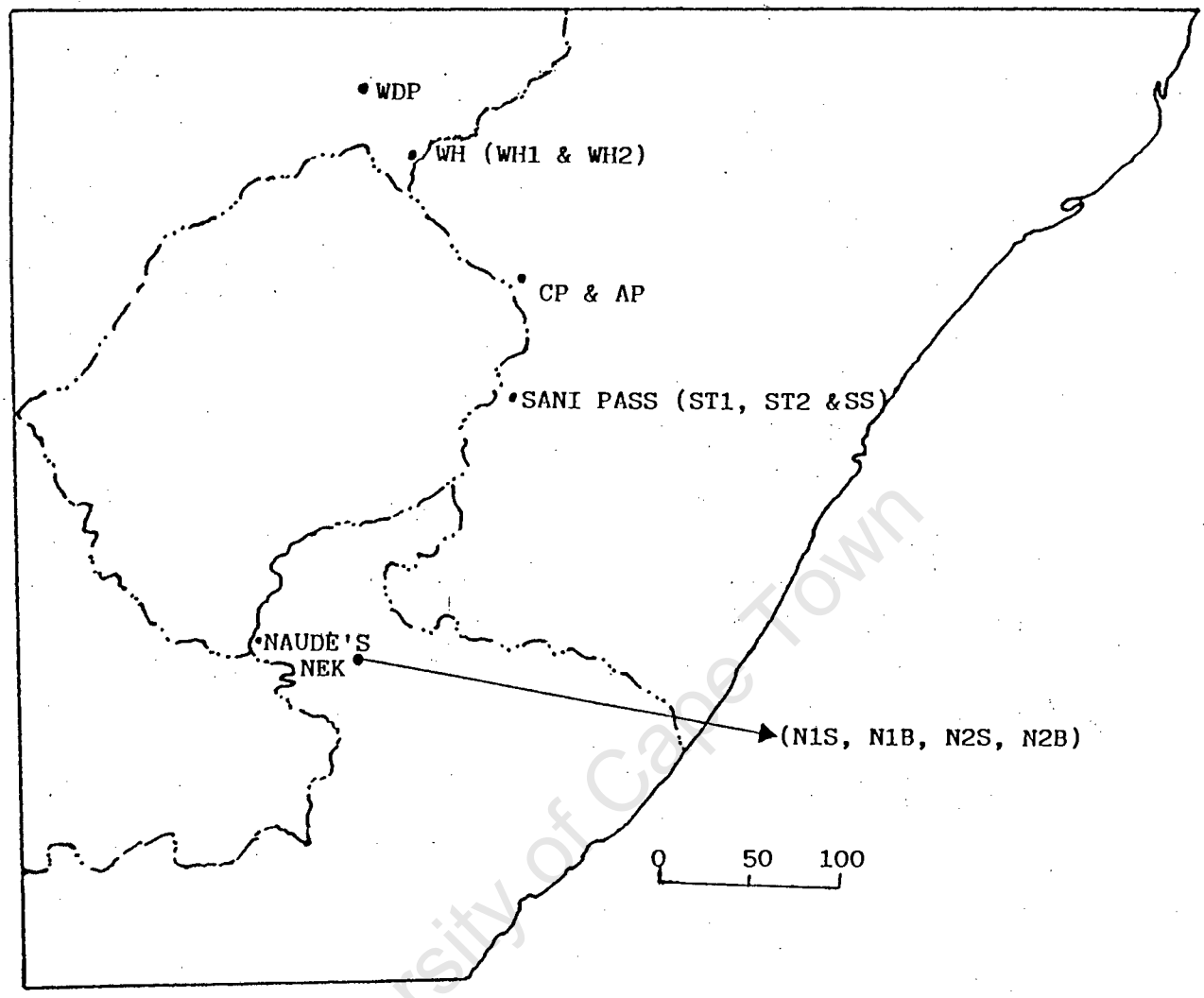


Fig. 1a . Map showing localities for populations sampled.

KEY TO PLACE NAMES

WDP = WODEHOUSE PEAK
WH1 = WITZIESHOEK POPULATION 1
WH2 = WITZIESHOEK POPULATION 2
CP = CATHEDRAL PEAK
AP = ORGAN PIPES
ST1 = SANI TOP POPULATION 1
ST2 = SANI TOP POPULATION 2
SS = SANI PASS SLOPE
N1S = NAUDE'S NEK POPULATION 1 (SMALL TUSSOCKS)
N1B = NAUDE'S NEK POPULATION 1 (BIG TUSSOCKS)
N2S = NAUDE'S NEK POPULATION 2 (SMALL TUSSOCKS)
N2B = NAUDE'S NEK POPULATION 2 (BIG TUSSOCKS)

Table 1: Site conditions for each sampling unit

* for explanation of codes.

Site *	Alt. (m.a.s.l.)	B \ U**	Plant size	Habitat***
1. Naude's Nek				
NN1	2250	B	Tall & Broad	D
NN2	2250	U	Short & Slender	D
N2B	2200	B	Tall & Broad	RW
N2S	2200	U	Short & Slender	RW
2. Sani Pass				
ST1	2865	U	Short & Slender	EDR
ST2	2865	U	Tall & Broad	PHB
SS	2750	B	Short & Slender	RW
3. Cathedral Peak				
CP	2950	U	Short & Slender	RW
AP	2750	U	Short & Slender	D
4. Witsieshoek				
WH1	2750	U	Medium	RW
WH2	2750	U	Tall & Broad	RW
5. Golden Gate				
WDH	1500	U	Tall & Broad	RWG

* N1S and N2S; adjacent populations with < 3m distance between them, N2B and N2S; adjacent populations with no distance between, about 15km from NN1 and NN2; ST1 and ST2, < 3m apart, SS about 5km from ST1 and ST2, Sani Pass more than 100km from Naudes Nek; CP and AP about 5 - 10 km apart; WH1 and WH2 adjacent; WDH, more than 100km from Witzieshoek.

** B = burnt in previous years; U = not burnt

***D = Dry area; RW = relatively wet area; EDR = exposed, dry rocky area; PHB = protected by *Helychrysum* bushes, RWG = relatively wet and protected gorge.

3.2. Sampling

A total of 297 individuals were sampled from these areas. The population size was not consistently large enough to allow the same sample size in all the populations. In all the areas, with one exception there was more than one population.

The sampling was done by drawing, randomly, an imaginary transact through the population in a straight line. Every second plant was sampled until the required sample size was obtained. The following characters were measured in the field: i)diameter of the tussock; ii) length of leaves (average length of leaves); and iii) length of culm including inflorescence. From each tussock a piece of leaf about 5 cm, from about the middle of the leaf, and a spikelet were preserved in FAA for all the samples. This was done to prevent repeating the measurements from a single plant/tussock, thus to avoid pseudo-replication. Every single tussock was sampled once because it was often difficult to ascertain whether leaves/culms from a given tussock belonged to a single plant or not.

The total number of characters measured is listed in Table 2. The characters studied were compiled from the characters used in the literature and also from those observed in the field and in the laboratory to show variation. Although the measurements and the analyses were done on pickled material, dried specimens were also

examined to ensure that the fresh material was representative of the species range. Spikelet and other morphological measurements were done in the laboratory under a dissecting microscope at variable magnifications depending on size. The herbarium specimens examined are housed at BOL and PRE. The data were subjected to several statistical methods for analysis.

3.3. **Leaf Anatomy**

From each of the plants sampled, a 2 cm length of leaf was fixed and stored in F.A.A. (20 alcohol (50%): 1 Acetic Acid: 1 Formalin). Leaves that were visibly unhealthy were avoided. Leaf cross sections were obtained by using two types of freezing stage microtomes; namely carbon dioxide microtome and an electrical microtome. These techniques are quick and they produce good results. For immediate data recording and examination, temporary mounts were made as follows: a section, 20 microns thick from one leaf per plant was made using the microtomes mentioned above. Staining was done by soaking the cross sections in toluidine blue for about two minutes. The cross sections were mounted in water and the coverslips were sealed with clear nail polish. The cross sections were examined immediately under a dissecting microscope at 50X. A flaw in this method is that the cross sections tend to open out, thus causing the width measurements of the cross sections to be impossible to carry out. The following measurements were taken: i) greatest half length of the cross section from the outer surface of midrib to the most distal epidermal cell, ii) thickness of the midrib, ii) thickness at the

narrowest point, iv) number of large vascular bundles, v) number of small vascular bundles, vi) number of ribs; vii) width of sclerenchyma at midrib region, viii) thickness of sclerenchyma at midrib region (Fig. 1b). Notes on the distribution of the sclerenchyma and variability in the shape of the cross section were taken.

A few permanent mounts of representative specimens were made as follows: The pieces of leaves that were soaked in F.A.A. were removed and rinsed in running water for one hour. They were then soaked in 40% Hydrofluoric acid for ninety minutes to remove silica bodies (Breakwell, 1914). The leaves were rinsed in water and subjected to a dehydration process (Feder and O'Brien, 1968) using a Sakura tissue processor as follows: two changes of eight hours each in :

i) 70% alcohol
ii) 100% alcohol
iii) n-propanol
iv) n-butanol.

After dehydration the pieces of leaves were embedded by soaking in two changes of melted pure wax (Paraplast+) for twenty four hours each. Cross sections about 20 microns thick were obtained using a sledge microtome. The cross sections were double stained in safranin and fast green (Johansen, 1940). They were then mounted in Depex. The epidermal scrapes were obtained by using the manual scraping method of Metcalfe (1960). The anatomical structures were recorded photographically. In leaf anatomical descriptions the terminology of Ellis (1976; 1979) is used.

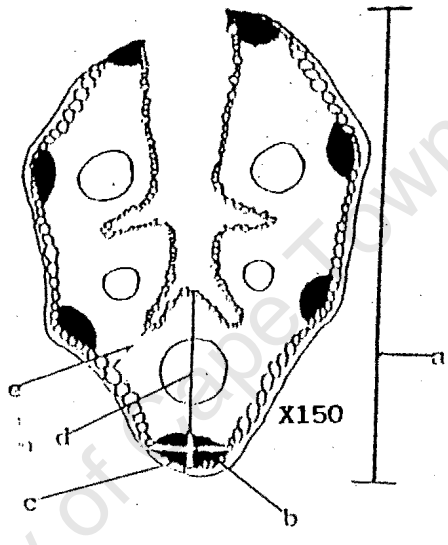


Fig.1b Camera lucida drawing showing measured characters of a leaf cross-section

a) greatest half length
b) width of sclerenchyma at midrib
c) Thickness of sclerenchyma at midrib
d) Thickness of midrib
e) Thickness at narrowest point.

3.4. STATISTICAL TECHNIQUES

The morphological and anatomical data were subjected to a number of statistical methods (viz): correspondence analysis using Underhill's Singular Value Decompositon Program (Underhill et al, 1985) run in a mainframe computer, cluster analysis using NTSYS-pc, ver. 1.40 (Rohlf, 1988) and Box and Whisker plots were generated using Statgraphics package in an IBM compatible micro-computer. Their results were compared to have a broad assessment of the total variation patterns. Anatomical characters were analysed separately from morphological characters as the sampling technique did not allow comparison of measurements from the same plant. These anatomical characters were not analysed further than the correspondence analysis.

3.4.1. CLUSTER ANALYSIS

Cluster analysis was performed on two different similarity matrices using NTSYS-pc programme, ver. 1.40 developed by Rohlf (1988). This programme performed this analysis by going through the following steps. It standardized the data and calculated the simalarity matrices using the Unweighted pair Group Method using Arithmetic Averages (Sneath and Sokal, 1973). These matrices are the taxonomic distance coefficient matrix and Pearson Product Moment correlation coefficient matrix. The matrices were based on morphological characters. Two phenograms were drawn from the values of the coefficients.

3.4.2. CORRESPONDENCE ANALYSIS

A correspondence analysis was also applied to the data. This technique permits the simultaneous plotting of samples and variables in a two dimensional space (Underhill et al, 1985). This programme standardises data so as to prevent excess weighting of some variables over others. The standardisation is such that the length of the vector from the origin to the points representing the morphological characters is proportional to the coefficient of variation of the character (Underhill, pers. comm). The program was run on a mainframe using Underhill's Singular Value Decomposition Programme (USVDP).

In this study the correspondence analysis can be thought of as a map of similarities between samples. Thus populations plotted close to each other are similar (in a certain sense). Loosely speaking, these populations are also correlated. This analysis is an improvement on a cluster analysis. The advantage of the correspondence analysis over a cluster analysis is that it does not only show which samples cluster but also what do they share in common (Underhill and Peisach, 1985). The correspondence analysis is a member of the family of statistical techniques whose similarity is calculating a singular value decomposition of a data matrix: (viz) Principal Components analysis; Factor analysis, the biplot and the canonical correlation analysis, (Underhill and Peisach,1985).

3.4.3. BOX AND WHISKER PLOTS

Box and Whisker plots are used to show variability between populations of the characters that were responsible for separating the clusters in the correspondence analysis and cluster. These characters are: leaf length, tussock diameter, awn length and lemma hairiness.

Table 2. Characters studied and used in the analysis

Estimated average leaf length (cm)	LL
Culm length (including inflorescence (cm)	CL
Tussock diameter (cm)	TD
Hairs on spikelets (lemmas and glumes, 6 states)	HL
glabrous 0	
scaberulous 1	
scabrid 2	
densely scabrid 3	
hairy 4	
densely hairy 5	
Awn length (mm)	AL
Lemma length (Lowermost lemma) (mm)	LL
Lemma width (on lowermost lemma) (mm)	LW
Spikelet length (mm)	SL
Number of Florets per spikelet	NF
Upper Glume length (mm)	UGL
Upper Glume width (mm)	UGW
Lower Glume length (mm)	LGL
Lower Glume width (mm)	LGW

First Rachilla segment (mm)	RS1
Second Rachilla segment (mm)	RS2
Greatest half length (mm)	GHL
Midrib Thickness (mm)	MT
Narrowest Point Thickness (mm)	NPT
Number of Large bundles	NLB
Number of Small bundles	NSB
Total number of ribs	TNR
Width of Midrib Sclerenchyma band	WSB
Thickness of Midrib Sclerenchyma band	TSB
Prickles/hairs on abaxial leaf surface	PBS
Prickles/hairs on adaxial leaf surface	PDS

3.5. Cytology

Seven populations were sampled for cytological study; four from Naude's Nek, three from Sani Pass. These populations form a subset of the populations sampled for the morphological and anatomical data, and were selected as they reflect the morphological variability across the collection sites. From each of these populations ten plants were selected randomly and potted in their own soil. These were grown in the university nursery. Voucher specimens were preserved from each population.

The immature inflorescences were obtained between 08h00 and 12h00. They were fixed immediately in Carnoy's fixative (60 absolute alcohol: 30 glacial acetic acid: 10 chloroform). Anthers were squashed and stained in formalin-lacto-propionic acid stain after twenty-four hours to three weeks of fixation. Temporal mounts of the preparations were made in the stain. Camera lucida

drawings were made using a Wild microscope.

3.6. Soil analysis

Soil samples from six populations, one from each population were collected. The soil was collected from the top 5 to 10 cm. The samples were stored in paper bags in room temperature conditions. These were air dried and analysed for pH, soil texture, soil moisture content, carbon content and phosphorus content.

CHAPTER 4: RESULTS

4.1. Taxonomy

Festuca caprina Nees, Fl. Afr. Austr. 443 (1841); Stapf, Thistleton-dyer FC VII: (1899); Burt-Davy, Checklist of Tvl & Swaziland, (1911); Phillips, Flora Leribe, 358 (1917); Bews, Flora Natal & Zululand, 38-48, (1921); Phillips, S.A. Grasses, 94 (1931); Chipp., Gr. and Past. S.A., 55 (1955); Martin & Noel, Albany & Bathust Flora, 20 (1960); Clayton, Gramineae. In F.T.E.A. , I, 62 (1970); Launert, FZ, 10 (1): 57 (1971); Guillarmod, Flora of Lesotho, 122 (1971); Ross, Flora Natal, 97 (1972); Compton, Flora of Swaziland, 57 (1976); Linder, Bothalia, (1986); Linder (Unpub.).

Type: Drege s.n. (PRE, ISO. !) S.A., Cape Province, Katberg, Queenstown.

Note: Another part of the isotype is at KEW (Linder, H.P., pers. comm.).

Synonymy

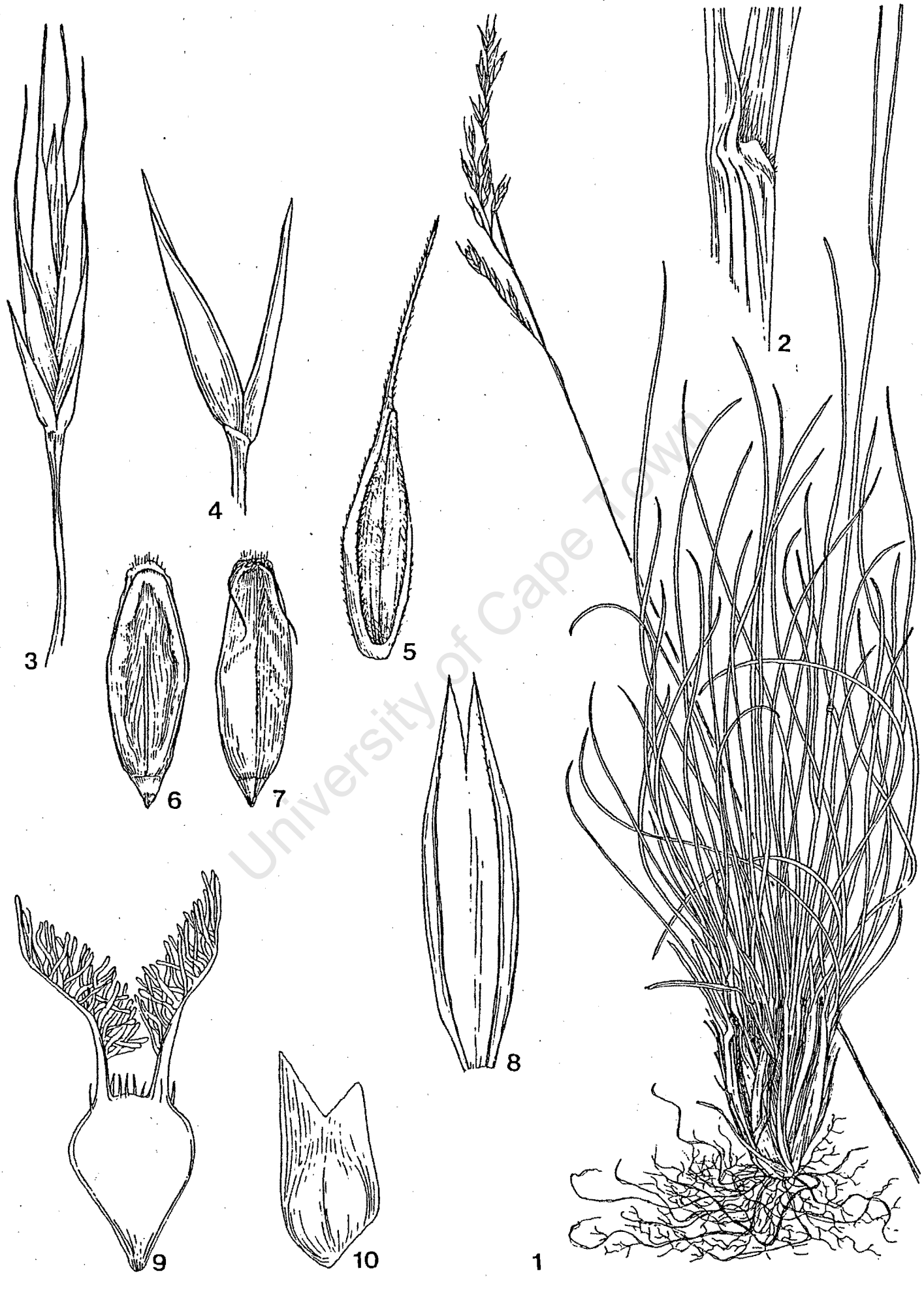
F. nubigena Jungh. ssp *caprina* (Nees) St. Yves in Rev. Bot. 2: 79(1927).

F. caprina Nees var. *irrasa* Stapf in Fl. Cap. VII (1899).

F. caprina Nees var. *macra* Stapf in Fl. Cap. VII (1899).

Plants perennial, densely caespitose, rarely loosely so. Culms slender, erect or rarely curved at base, base covered with old fibrous, brownish leaf sheaths, 0.21 -- 1.05m high; simple with approximately 2 - 3 nodes; surface ribbed, nitid; apical inter-

node exposed from halfway up. **Leaves** basal; sheaths tightly rolled around the culms, glabrous; blades filiform and involute, glabrous, scabrid above, 40 - - 400mm long and up to 1.3mm wide; ligule glabrous entire, ciliate at apex, up to 1mm long. **Inflorescence** contracted or open and spreading, sometimes drooping on one side, narrowly ovate when contracted to broadly so when open; nodes 4 - 12; rachis glabrous, scabrid, or puberulous; branches filiform, in alternate pairs or solitary. **Pedicels** conspicuous, glabrous, scabrid or puberulous, apex gradually thickened. **Spikelets** pedicellate, numerous, oblong, 4 - 9 flowered, pale green to dark green, sometimes with purple variegation, 6.5 -- 14.5mm long. **Glumes** unequal, glabrous to pubescent, lower 2 -- 5.5mm long, lanceolate, 1-nerved; upper 3 -- 6.5mm long, lanceolate to broadly ovate, 3 -nerved. **Callus** glabrous. **Rachilla** glabrous to puberulous, 1 -- 3mm long. **Lemmas** ovate, glabrous, scabrid or pubescent; apex entire or acuminately bilobed, 5 -- 10mm long, 5 - 7 nerved middle nerve excurrent into an awn. **Awn** straight, 1 -- 5.5mm long. **Lodicule** up to 1.5mm long, fleshy at base, membranous above, lobed or not lobed. **Palea** two keeled, glabrous, scarious at keels, as long as lemma or slightly shorter. **Anthers** 3, 1.5 - 2mm long. **Stigmas** 2, plumose. **Ovary** obovoid, hairy on top. **Caryopsis** oblong, rounded on embryo side, ventrally sulcate, hilum linear, as long as or slightly shorter than the fruit. (see Figs. 1-10).



Figs. 1—10. Morphology of Festuca caprina.

THE CARYOPSIS

In this study no variation was observed in the caryopsis between populations but for a slight change in size. This change corresponds to differences in lemma size.

The caropsis is linear to slightly narrowly lanceolate in outline sometimes broadening slightly at the base. The dorsal side is convex and sulcate on the ventral side. The embryo is less than 1/4 of the caryopsis and conspicuously dermacated from the rest of the fruit. It is obovate in shape. The hilum is linear, as long as the full size or 3/4 of the full size. It rests in a groove, uniformly deep. The width of the groove varies according to the width of the caryopsis. Sometimes there are hairs on the stylar end. However, the presence of these hairs seems to be determined by the stage at which the caryopsis was dried. Younger caryopses tend to have conspicuous hairs, these may be lost with age. The coat sculpturing is irregular although it tends towards striate.

Vouchers: Sokutu 104, 115, 119; (BOL)

KEY TO FIGURES 1-10. Drawings showing morphology of *Festuca caprina*.

1 = Whole Plant (X1)

2 = Ligule (X14)

3 = Spikelet (X16)

4 = Upper and Lower glumes (X33)

5 = Lemma, ventral side (X11)

6 = Fruit with remains of ovary, ventral side (X17)

7 = Fruit with remains of ovary, dorsal side (X17)

8 = Palea, ventral side (X15)

9 = ovary with stigmata and ovary on top (X40)

10= Lodicule (X50)

4.2. The disarticulation of spikelets

The disarticulation of the spikelet takes place above the glumes. The spikelet falls at maturity leaving the long persistent glumes on the culm. The persistence of the culm long after the growth season makes it easier to identify *Festuca caprina* from vegetative material in the field. From the caryopses that were collected from the field and air dried, it seems as if no further disarticulation occurs between the florets. This may not be so in the field since different factors like moisture may play a different role. It has been reported that disarticulation in the genus *Festuca* takes place above the glumes and between the florets. The florets containing the caryopses seem to remain enclosed until the palea and the lemma decay. This gives a chance for the caryopsis to germinate. Lemma and palea remained stuck to the caryopsis long after they were air dried.

4.3. Leaf Anatomy

Outline of cross section: reduced v-shaped to u-shaped, arms straight to angular, or elliptical forming an incomplete oval or ellipse, sometimes margins overlapping slightly. **Adaxial ribs and furrows:** ribs present opposite all vascular bundles, cleft-like or slightly rounded, furrows narrow sometimes slightly wide, deep or shallow. No abaxial ribs and furrows. **Median vascular bundle:** not structurally distinct from but sometimes slightly bigger than

lateral vascular bundles. **Vascular bundle arrangement:** follows a basic pattern i.e always 3 first order bundles and two or four second order vascular bundles, when 2 second order vascular bundles are present there is one between consecutive first order vascular bundles. Vascular bundles vary in number, 5 or 7. All vascular bundles situated in the centre of the blade. **Vascular bundle shape:** round to obovate. Phloem sometimes lignified, adjoined to inner bundle sheath; metaxylem cells conspicuous, three or four: two lateral; one on either side, one or two slightly above the centre. **Vascular bundle sheath:** double, outer bundle sheath composed of parenchyma cells, more or less isodiametric, abaxial side lack any outer bundle sheath cells, cells smaller than the mesophyll cells, lacking chloroplasts; mestome sheath irregularly thickened on inner tangential and radial walls. **Sclerenchyma:** limited in extent, adjacent to the abaxial epidermis opposite each vascular bundle and as tiny caps at margins, sometimes thicker at the midrib. **Mesophyll:** irregular tending to a radiate condition. Cell shape irregular, varying from round to elongate. Lateral cell count more than 4, continuous between bundles, inter-cellular spaces not frequent. **Adaxial epidermis:** cells very small, stomata sunken, more frequent in furrows, bulliform cells in threes at bases of furrows, not distinct. Cuticle thin or a thick layer, prickles absent to few. **Abaxial epidermis:** cells bigger than those of adaxial epidermis, sometimes periclinally thickened.

4.3.1. Surface view

Abaxial intercostal long cells elongate, rectangular, walls

straight to sinuous. Cell size variable within and between intercostal zones, sometimes fairly consistent across individual intercostal zones, long cells adjoin one another, sometimes separated by short silica and cork cells, these adjoined to one another. Neither bulliform cells nor stomata on abaxial epidermis.

Adaxial long cells elongate, walls straight. Stomata interspersed among the epidermal cells randomly throughout the surface view, rectangular or dome shaped, subsidiary cells more or less parallel sided.

Flowering time: December to February

Distribution: Eastern Cape, Barkly East to Natal, O.F.S., eastern Transvaal, Swaziland, north to southern Tanzania. (see Fig. 1c for South African distribution).

4.4. SOME OBSERVATIONS OF NATURAL POPULATIONS

F. caprina occurs on afroalpine and afromontane grasslands (Killick, 1978) from about 1500m - 3000m a.s.l. (Hillard and Burtt, 1986; pers. obs.). Its populations occur as dominant and even important constituents of its habitats. These populations grow on basalt bedrock type, on black rich soil. The soil is classified as Mountain Black Clay (van der Merwe in Killick, 1963). At least one population was found on a rocky slope. The individuals in this population are distinctly smaller than others.

Another population which grows a few metres away from its rocky

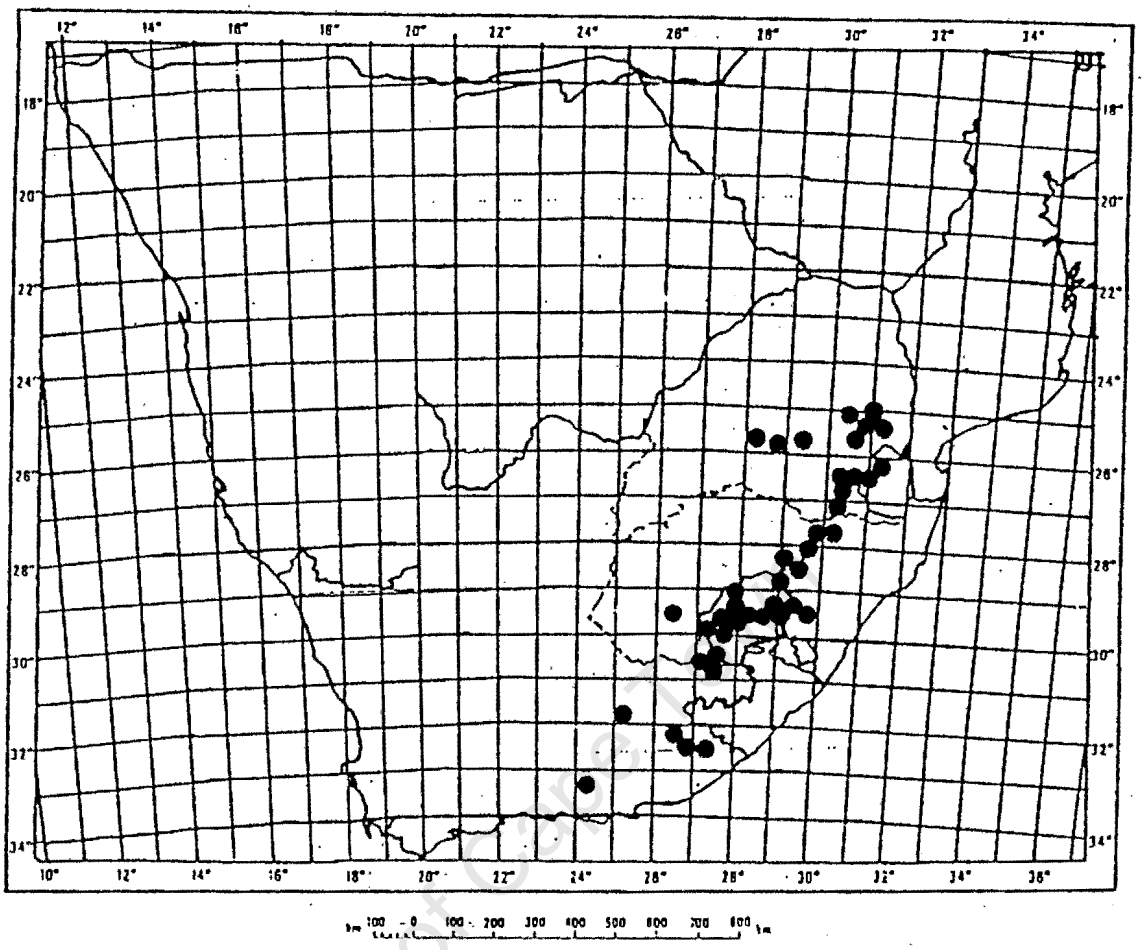


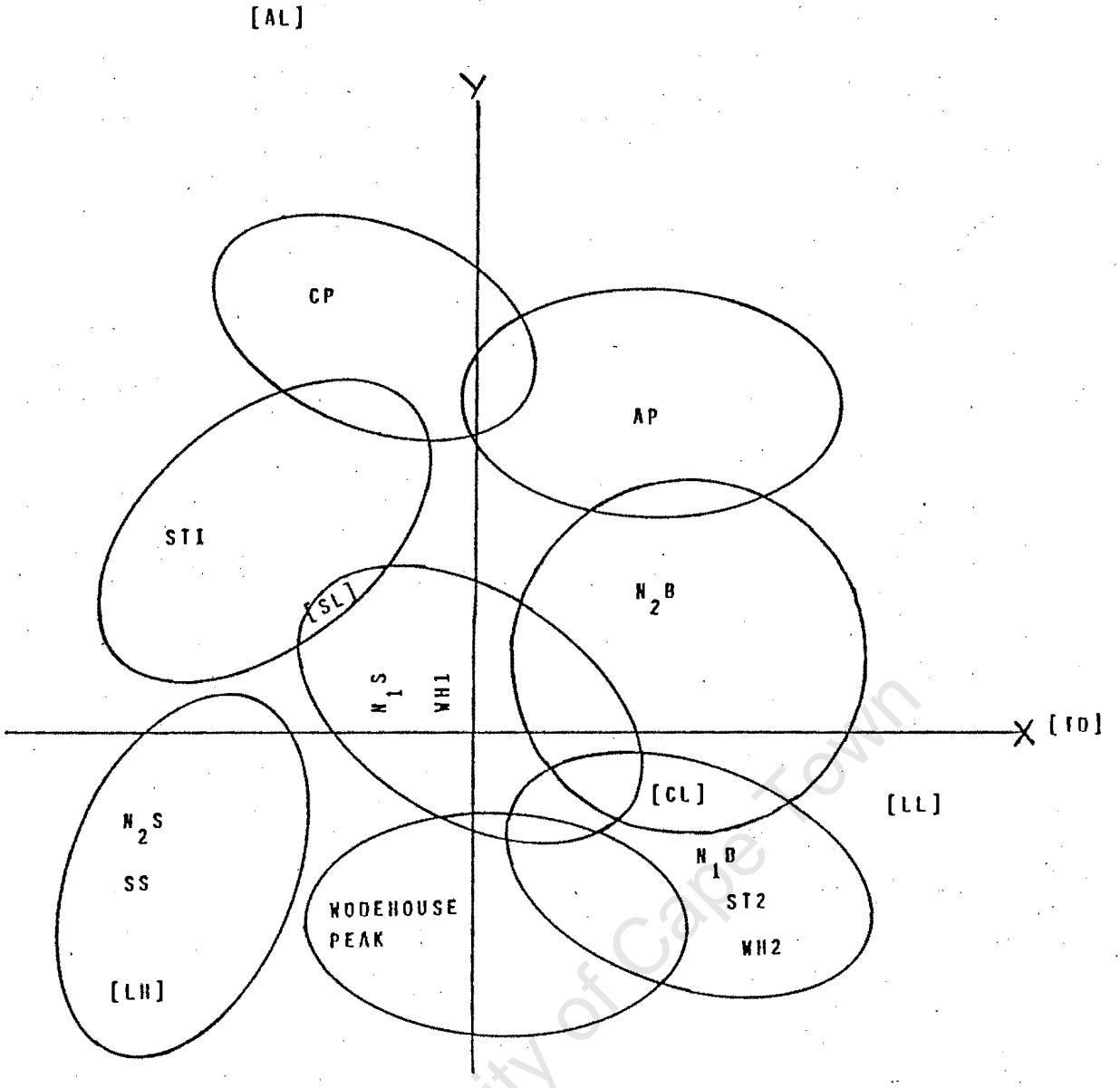
Fig. 1c. Known geographical distribution of Festuca caprina in southern Africa.

slope neighbour through the shade of *Helichrysum* bushes, has a distinctly different appearance. Sometimes *F. caprina* populations occur along streams on very wet places, boulder beds, cliff faces and valley bottoms. In some cases the populations appeared to have been subjected to fire and/or grazing in the past.

It is not clear whether the differences between some populations are due to different fire regimes or whether they are merely coincidental. This is especially so between populations which either have not been subjected to fire or have all been subjected to fire, but are different from each other. The ecological preferences of the different morphotypes did not seem to differ and are therefore not important in population differentiation.

4.5. THE CORRESPONDENCE ANALYSIS

Fig. 13 shows the distribution of taxa according to their morphological characters as displayed by the Correspondence analysis. From the graphical display it can be seen that different populations form clusters in different positions. Depending on their measurement values those populations which are similar to each other tend to overlap in varying degrees. Therefore the degree of overlapping between clusters represents the degree of similarity between populations represented by those clusters. Table 3 shows the percentage variance represented by each axis. Axis 1 accounts for 44.07% of the total variability and axis 2 for 19.67% variability. Thus the two axes displayed represent 63.74% of the variability in all the fifteen axes. The



CP = Cathedral Peak
ST1 = Sani Top 1
ST2 = Sani Top 2
AP = Organ Pipes
N_1S = Naude's Nek 1 (small tussock)
N_1B = Naude's Nek 1 (Big tussock)
N_2S = Naude's Nek 2 (Small tussock)
N_2B = Naude's Nek 2 (Big tussock)
SS = Sani Pass Slope
WH1 = Wietzieshoek 1
WH2 = Wietzieshoek 2
WDH = Wodehouse Peak

[LH] = Hairyness on lemmas
[AL] = Awn Length
[CL] = Culm length
[LL] = Leaf length
[TD] = Tussock Diameter

Fig. 13. Correspondence Analysis based on a 295 X 15 Morphological data matrix.

third axis contributes an additional 8.7% of the total variability. The percentage contribution of the other twelve axes ranges from 7.46% to 0.00%.

Table 4 shows that the leaf length, tussock diameter and lemma hairiness make the highest percentage contributions: (22.7%, 46.8% and 17.2% respectively) to the first axis. The variability in the second axis is mainly due to lemma hairiness and awn length with contributions of 14.2% and 73.0% respectively (see Fig. 13 for graphic display). The other characters do not seem to contribute significantly to the total variability. Thus the leaf length, tussock diameter, lemma hairiness and awn length are mainly responsible for revealing the different populations.

Table 3. Morphological characters

THE PERCENTAGE VARIANCE REPRESENTED BY EACH AXIS

AXIS	PROPORTION	CUMULATIVE PROPORTION
1	44.07	44.07
2	19.67	63.74
3	8.71	72.46
4	7.46	79.92
5	6.53	86.45
6	3.36	89.81
7	2.87	92.69
8	2.49	95.19
9	1.67	96.86

10	1.09	97.95
11	.89	98.84
12	.48	99.33
13	.37	99.70
14	.30	100.00
15	.00	100.00

Table 4. Morphological characters

PERCENTAGE CONTRIBUTIONS OF VARIABLES TO EACH AXIS

		AXIS 1	AXIS 2
NAME	SYMBOL	% CTR	% CTR
LEAF LENGTH	LL	22.7	0.5
CULM LENGTH	CL	4.2	0.2
TUSSOCK DIAMETER	TD	46.8	0.0
LEMMA HAIRINESS	LH	17.2	14.2
AWN LENGTH	AL	2.2	73.0
LEMMA LENGTH	LE	0.7	1.6
SPIKELET LENGTH	SL	0.8	3.6
NO. FLORETS	FN	1.4	0.0
UPPER GLUME LENGTH	UGL	0.5	0.4
LOWER GLUME LENGTH	LGL	0.7	0.8
LEMMA WIDTH	LW	0.5	1.9
RACHILLA SEGMENT 1	RS1	0.8	0.4
RACHILLA SEGMENT 2	RS2	0.8	0.3
UPPER GLUME WIDTH	UGW	0.2	1.9
LOWER GLUME WIDTH	LGW	0.4	1.1

Table 5. Anatomical characters

THE PERCENTAGE VARIANCE REPRESENTED BY EACH AXIS

AXIS	PROPORTION	CUMULATIVE PROPORTION
1	68.16	68.16
2	20.04	88.20
3	5.74	93.94
4	2.17	96.11
5	1.53	97.64
6	1.28	98.94
7	.65	99.60
8	.35	99.95
9	.05	100.00
10	.00	100.00

Figure 14 displays the distribution of clusters according to anatomical characters. Table 5 shows the percentage variance represented by each axis. Table 6 shows the percentage contributions of anatomical variables to each axis.

4.6. CLUSTER ANALYSIS

The two phenograms in Fig. 15 show the distribution of the taxa according to their morphological characters. Fig. 15a is based on taxonomic distances between samples and Fig. 15b is based on Pearson Product moment correlation coefficient. The cophenetic correlation coefficients (r) for these phenograms are 0.83 and 0.86 respectively. Anatomical characters were not analysed further than the correspondence analysis since they do not seem to play an important role in the species variation.

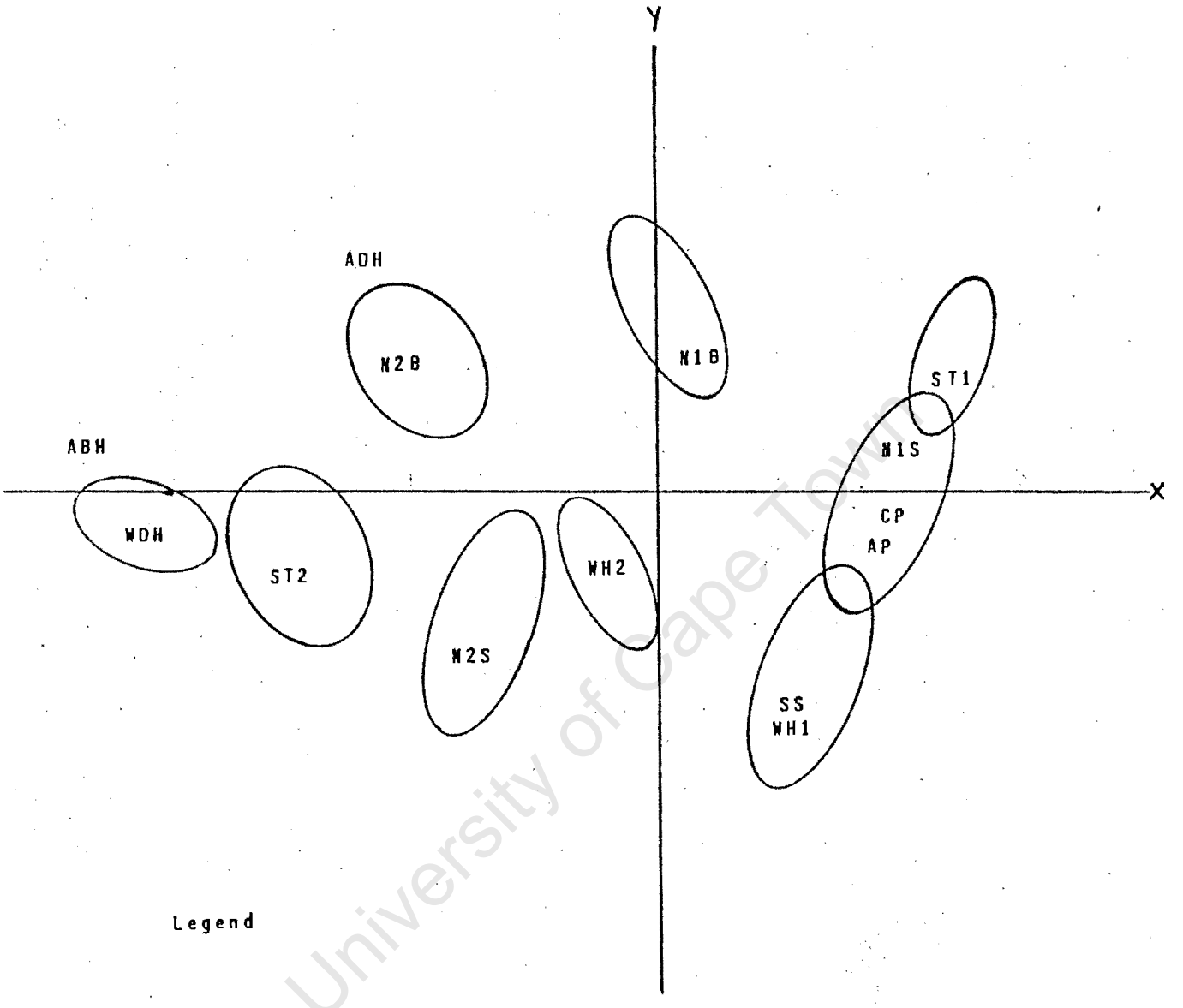


Fig. 14. Correspondence Analysis based on a 250 X 10 anatomical data matrix.

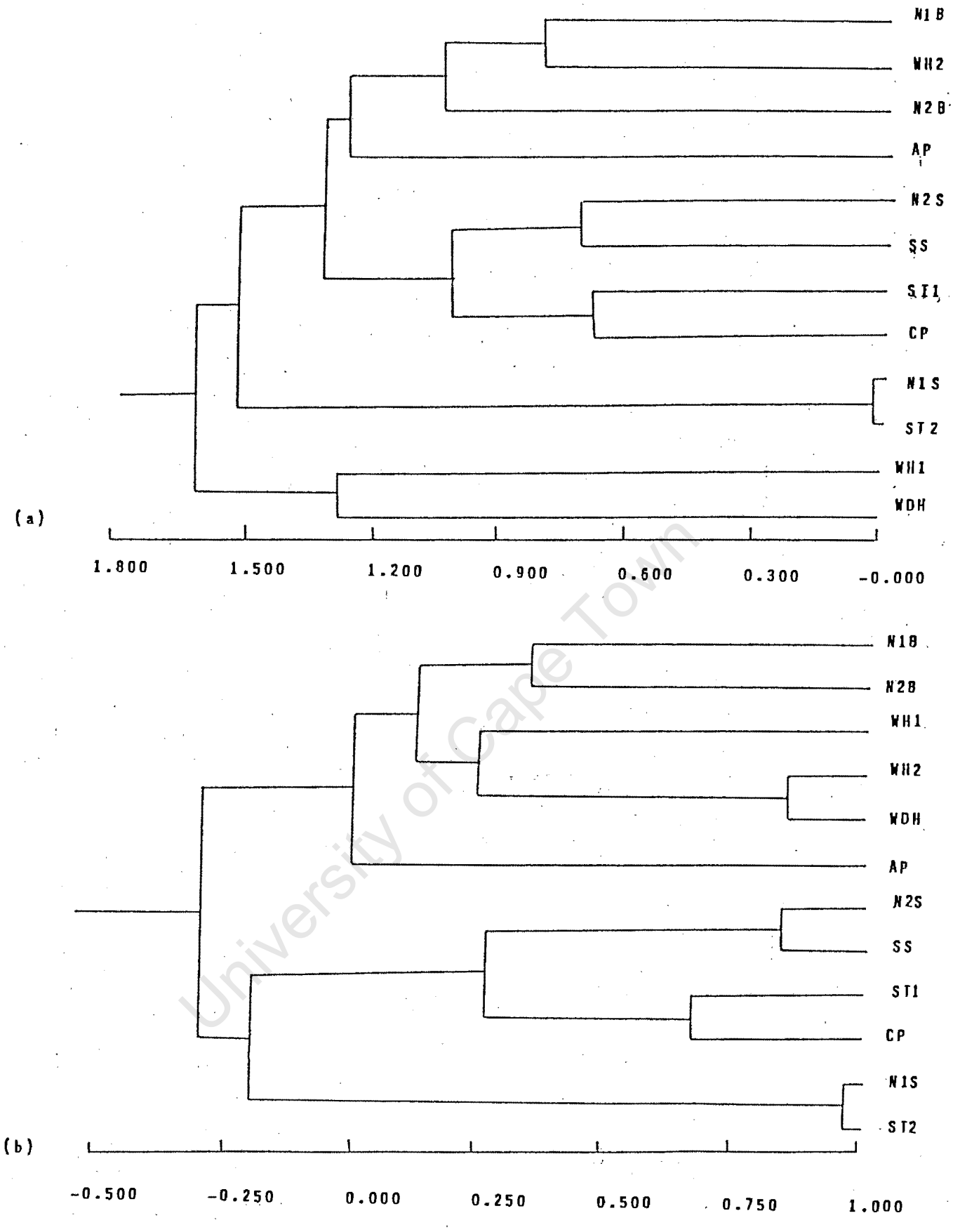


Fig. 15. Phenograms based on morphological characters; (a) Taxonomic distance, (r=0,85); (b) Pearson Product moment correlation coefficient, (r=0,83).

4.7. BOX AND WHISKER PLOTS

The Box and Whisker plots (Fig. 16a-d) show the variation of four characters between populations, where populations are represented by the following numbers:

1 = Naude's Nek, locality 1, small tussocks (N1S)
2 = Naude's Nek, locality 2, big tussocks (N2B)
3 = Naude's Nek, locality 2, small tussocks (N2S)
4 = Sani Pass Top, population 1 (ST1)
5 = Sani Pass Slope (SS)
6 = Organ Pipes (AP)
7 = Witzieshoek, population 1 (WH1)
8 = Witzieshoek, population 2 (WH2)
9 = Wodehouse Peak (WDH)
10 = Naude's Nek, locality 1, big tussocks (N1B)
11 = Sani Pass Top, population 2 (ST2)
12 = Cathedral Peak (CP)

Only the most variable characters are shown. It can be seen that there are sharper differences between populations from the same area than from different areas. The Box and Whisker method was not used in Fig. 16c because the lemma hairiness remained constant in each population.

4.8 CYTOLOGY

The task of chromosome number determination was very difficult mainly due to the very small size of the chromosomes but also because in most cases the chromosomes just could not be seen. However, this was a pilot study to show that the techniques

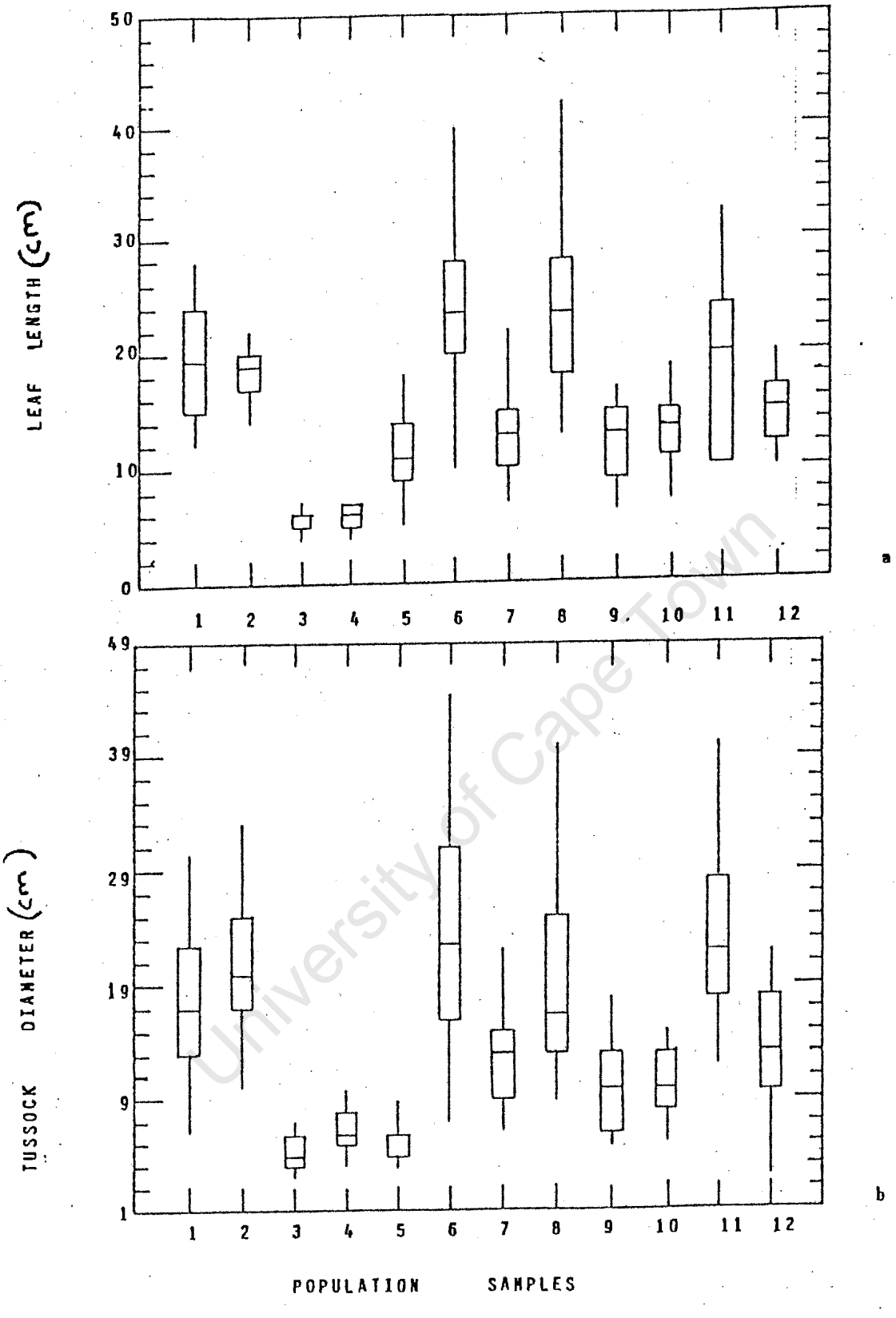


Fig. 16a- b. Box and Whisker plots showing variation between populations in (a) Leaf length (b) Tussock diameter

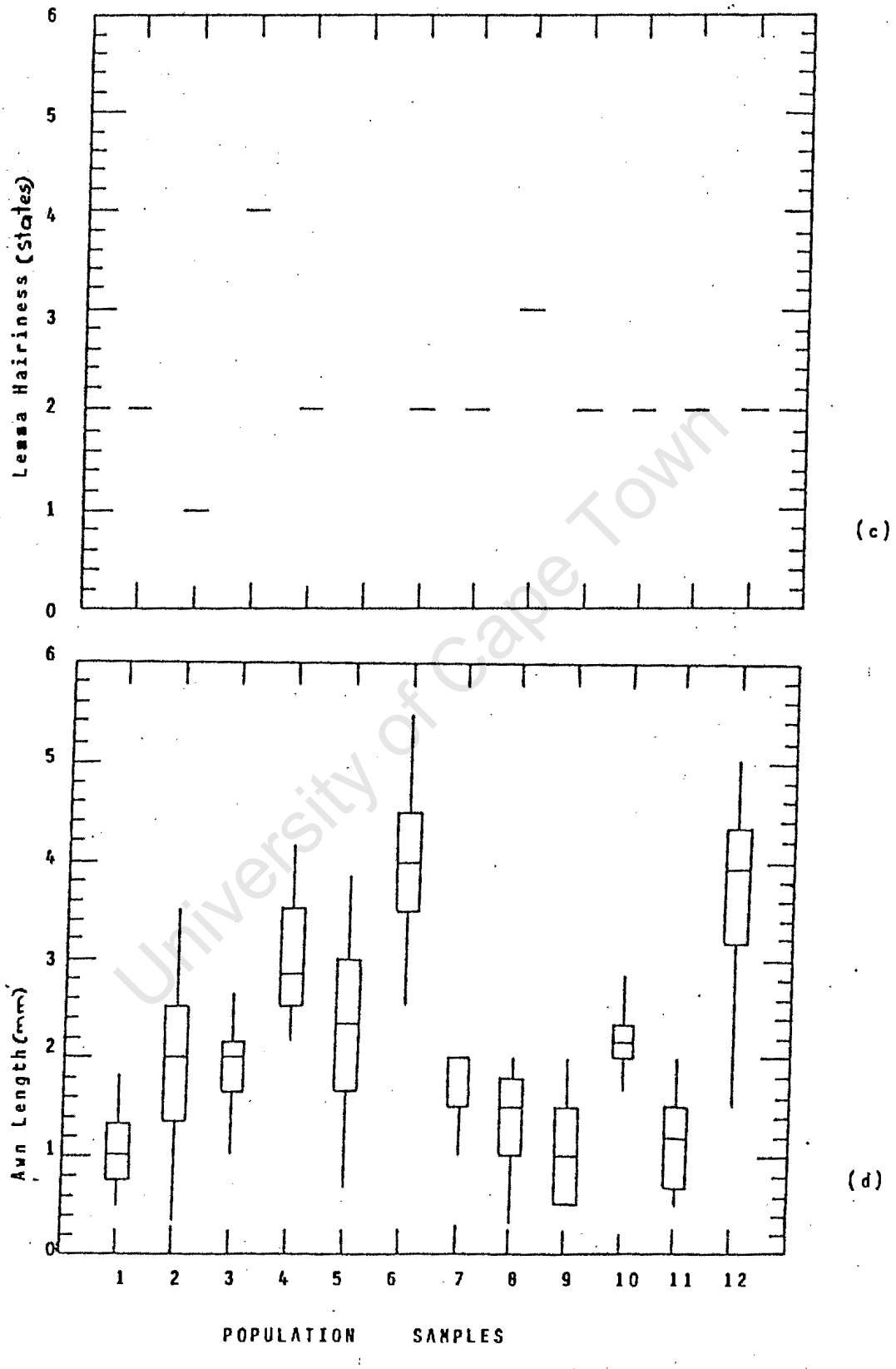


Fig. 16c – d. Box and Whisker plots showing variation between populations in (c) Lemma hairiness, (d) Awn length.

employed work in this species.

Three of the seven samples did not flower in the nursery. Of the four that flowered, the numbers of chromosomes could be successfully determined only from two samples. One of the other two was dubious and the last one was not successful.

Both determinations indicated that those population samples were tetraploids (n = 28) (Fig. 17). No abnormal chromosomes were observed. The shape of the chromosomes was not always clear although they tended towards a very short v-shape with a median centromere.

4.9. Soil Analysis

The results of soil analysis are shown in table 8 below.

Table 8. Results of Soil Analysis

Sample	Soil pH (K=1.10, 25)	Elec. Cond.	%H O	%Carbon	P
N2B	5.4	370	18.42	15.8	.400
ST2	4.8	192	45.1	25.8	.671
SS	4.7	265	32.3	38.2	.505
N2S	5.9	474	18.42	15.8	.444
N2B (S)	4.8	185	32.3	17.6	.755
N2S	5.2	205	32.3	11.7	.813
ST1	4.9	129	29.6	10.2	.249

Key:Elec. Cond. = electrical conductivity, P = Phosphorus.

Fig. 17. Camera lucida drawing showing chromosomes (n = 28) at metaphase 1.

CHAPTER 5: DISCUSSION AND CONCLUSIONS

5.1. DISCUSSION

The display of the correspondence analysis in Fig. 13 shows the distribution of clusters according to morphological variation. A number of features can be observed in this display, including:

i) distribution of variation between and within populations,
ii) the relationship between the distribution of clusters according to the display and their geographical distribution and associated environmental factors e.g. soils,
iii) the characters responsible for the pattern of variation and
iv) possible explanation for the displayed distribution.

The clusters in Fig. 13 are distributed around the two axes according to their morphological similarity. Those clusters that lie close to each other on the display are morphologically similar to each other. The display shows that all the clusters but one overlap with each other. The degree of overlap differs between clusters indicating that the degree to which the clusters are similar to each other varies. The display therefore indicates that there is continuity between the clusters which reflect continuity between the populations sampled. Similarly, the populations represented by those clusters that are similar to each other are also correlated. It must, however be borne in mind that some cluster positions may be distorted since they are compressed to two dimensions. Therefore the exact correlations should be checked from the correlation coefficient table.

The clusters representing the distribution of the populations of *F. caprina* in the Correspondence Analysis are scattered around the two axes. This shows that although there is continuity between populations on the one hand, they are fairly dissimilar. FOn the other hand the distribution of the actual data points in the display shows that there is limited variability within each population, resulting in each population being more or less uniform.

The distribution of the clusters according to morphological characters in Fig. 13 shows that the population samples that are similar to each other are not necessarily from the same locality. Fig. 14 also shows this feature. The populations from the same locality differ from each other in most cases. For example, population samples from Naude's Nek (N2S) and Sani Pass (SS) slope have a 100% overlap. The same is true for populations from Naude's Nek (N1B), Sani top (ST2) and Witzieshoek (WH2). The display shows therefore, that there is no correlation between the geographical (different mountain blocks) distribution and the population distribution. Therefore population differences within and between localities are not related to the corresponding geographical distances. For example, the populations from Sani Pass top with a distance of about two metres between them are dissimilar and therefore negatively correlated. On the other hand some populations from localities further apart from each other may be similar and correlated to each other e.g. Cathedral Peak (CP), Witzieshoek, Sani Pass and Naude's Nek, (see fig. 13, 15 and 16).

The clusters according to the phenograms also show a similar situation, (fig. 15). The clusters correspond neither to geographical regions, nor to environmental differences. Populations from the same locality are scattered through the phenograms. These populations are separated by sharp boundaries, within one locality, in terms of their phenotypic appearances. Two major groups can be recognised in Fig. 15a. These are those clusters representing populations with big and small tussocks respectively. The populations with big tussocks are grouped together and the populations with small tussocks and long awns are grouped together. These groups are not clearly defined because the joining levels are relatively low. The small group formed by populations from Naude's Nek 2 and Sani Pass indicates that these populations are highly similar to each other. This result is surprising when the results from the correspondence analysis and the field observation are taken into account. These groups visually belong to the small and big tussock groups respectively. I suggest that this distortion is due to the fact that this analysis is based upon averages of the variables only, and therefore some information may be lost in cases where the extreme values affect the entire data. On the whole, these results are similar to those of the correspondence analysis in that groups with big tussocks are separated from those with the small tussocks and (see Fig. 15a) negatively correlated to each other (see Fig. 15b), irrespective of their habitats.

In order to look at the coefficient of variations of each character, an average of each character is considered. A length of the line drawn from the origin to the symbol representing the

character mean approximates a standard deviation of that character. Thus the shorter the line, the lower the variability and vice versa (Barr, Underhill and Kahn, unpub.). This feature can also be checked against the table of standard deviations values. Thus the population from Witzieshoek (WH1) and from Naude's Nek (NiS) have the lowest variability while the population from Sani Pass top (ST2) has the highest variability. The cosine of the angle subtended by any of these two lines at the origin approximates correlation between the populations to which the character means belong. Thus a small acute angle indicates positive and large correlation, while a right angle indicates zero correlation, and an obtuse angle indicates a negative correlation (Wandt and Underhill, 1988), (See figure 18). It must be borne in mind that some population positions in the display may be distorted since they are compressed to two dimensions. Therefore the exact correlations should be checked from the correlation coefficients table.

The questions that need to be answered now are "Which characters are responsible for the distribution of the clusters in Fig. 13.? Are the same characters responsible the distribution of clusters in the phenograms?" The percentage contributions of variables to each axis (Table 4) show that the variables that are mostly responsible for the distribution of clusters according to Fig. 13 are: leaf length (22.7% in axis 1); tussock diameter (46.8% in axis 1); lemma hairiness (17.2% in axis 1 and 14.2% in axis 2) and awn length (73.0% in axis 2). Fig. 16 a - d shows the variation of these characters between populations. Other characters,

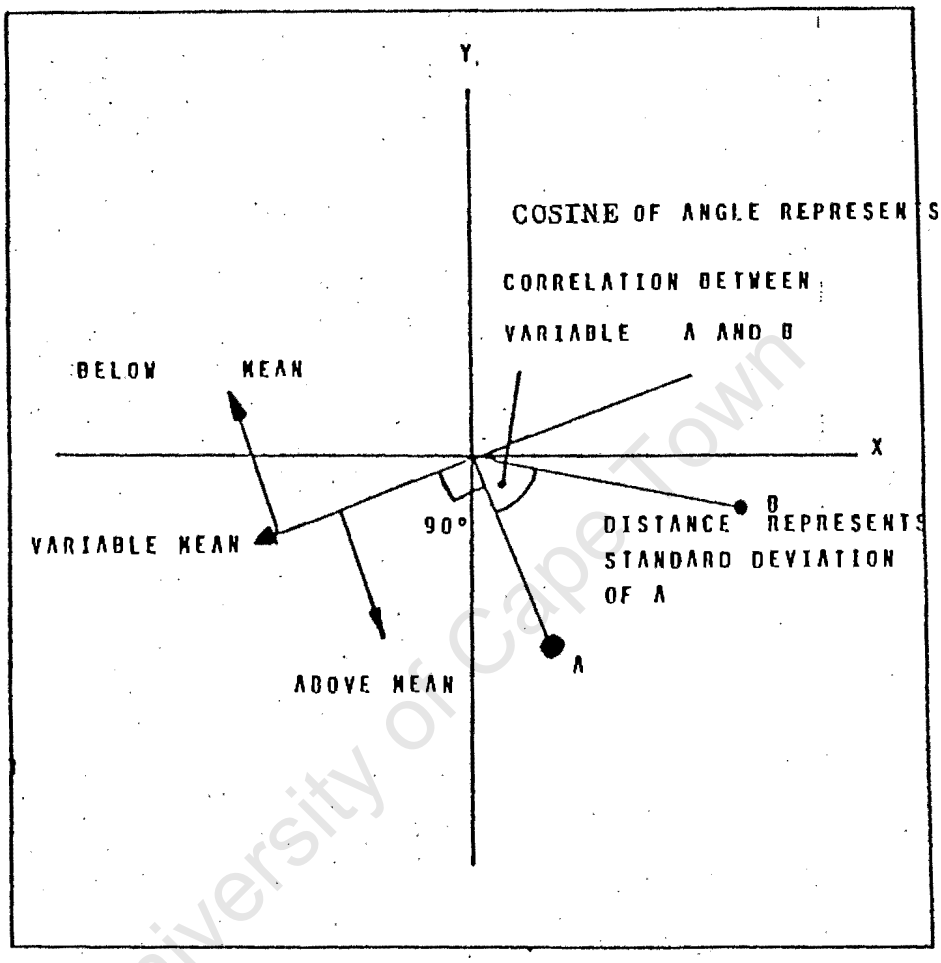


Fig. 18. Diagram to show information contained in a display of Correspondence Analysis.

mainly the reproductive characters do not seem to play a significant role in separating these populations. Spikelet characters have been used below species level in the past to isolate groups within species, since they are considerably less variable than vegetative characters (Harberd, 1961; Harberd and Owen, 1969; Brown et al., 1978; Shaw and Smeins, 1979; Doebly and Iltis, 1980; Pavlick and Looman, 1984; Baum and Bailey, 1988;). The fact that they do not play an important role here may be an indication that there are no groups within *F. caprina*

Only the characters that play a significant role in the population variability are plotted in Fig. 13. Other characters were almost all clustered towards the centre of the display. This relationship is very interesting because it means that the characters that are variable are the vegetative characters.

Populations from Naude's Nek (N1B), Sani Top (ST2), and Witzieshoek (WH2) have a 100% overlap sharing high values of lemma length, tussock diameter and culm length. Also population samples from Naude's Nek (N2S) and Sani Pass (SS) slope have a 100% overlap. They share high values of lemma hairiness. Similarly, populations from Sani Top (ST1) and Cathedral Peak (CP) share high values of awn length and low values of tussock diameter, leaf length and culm length. Since the latter characters are plotted close to each other, they are more correlated to each other than they are to awn length which is plotted on the other end of the display. Therefore the clusters that share high values of these variables are more correlated to each other than those that share high values of awn length. It

seems therefore that the plant size decreases as one moves up the y-axis while the awn length increases.

The leaf length (LL) and the tussock diameter (TD) show the highest correlation coefficient. At the same time these two characters have the highest variability as measured by the coefficient of variation. Therefore it is expected that the differences between populations are mainly due to differences between these two characters. Thus populations which have a high correlation should be more similar to each other with respect to these characters and vice versa. The display indicates that this is the case.

The plot in Fig. 14 shows that the populations are separated by the amount of abaxial hairiness. Table 4 shows that this variable contributed 83% of the total variation. Axis one and two captured 88.20% of the total variation, (table 5). Thus the populations on the extreme left of axis 1 share the highest values of abaxial hairiness while those on the extreme right share the lowest values. This result was unexpected since all populations did not have significant amounts of hair on the leaves. It is suspected that the coding of the amount of hair might have distorted the real picture. However none of the other characters played an important role in this variation (see table 4).

The results show that *F. caprina* is a variable species . The variation is reflected in such characters as the tussock size, leaf length, awn length and culm length. However the variation pattern is such that there is a continuum from one morphological extreme to another, i.e solitary plants with short leaves to big

tussock forming plants with long leaves.

The study also showed that there is a positive correlation between plants with big tussocks long leaves and long culms and also between short plants (short leaves, small tussocks) and awn length. The other character which was taken note of is the degree of spreading of the inflorescences. In most populations the inflorescence is compact and closed, whereas in others it is loose and spreading. This has no correlation to awn length.

There also seems to be a positive correlation between the degree of spreading of inflorescence and the height of the plants. Spreading inflorescences were only observed in tall plants although they were also observed to possess closed and compact inflorescences. The populations that possess densely pubescent spikelets are only those with solitary plants with short leaves. Only two populations of these were observed.

Each population reflected, as observed in the field, a high degree of homogeneity such that if all the localities for the plants are known with field experience, accurate prediction of the plants locality can be made. The populations showed very sharp boundaries from one population to an adjacent one. For the characters studied the order of contribution to variation is as follows:

between populations > between regions > within populations.

What can be a possible explanation of the variability discussed above?. The two populations that were successfully determined for chromosome counts have different morphological expressions al-

though they both represent small tussocks (ST1 and N2S). These chromosome counts agree with counts previously published by Spies and Du Plessis (1986). They reported two counts from the Transvaal area. In one of these counts they reported 2 beta chromosomes (n = 28 + 2). It is difficult from the chromosome counts to say whether *F. caprina* is a polyploid complex or not since it was not possible to determine the whole variation range.

The variability in this species may be the product of phenotypic plasticity and genotypic variability: Populations from Sani Pass, ST1 and ST2, were found on two different habitats. One population grows on exposed rocky surface and adjacent to it is another growing through *Helychrysum* bushes. The latter therefore had a protected habitat resulting in a cool, relatively humid, probably more nutrient rich micro-habitat in contrast to its neighbour, on dry rocky habitat. This is confirmed by the results of the soil analysis (see table 8). These results indicate that there are no differences or there are small differences between soil samples. Overall when considering pH, electrical conductivity, percentage water content, % carbon and phosphorus, there seems to be similarity between adjacent habitats. The differences between ST1 and ST2 in terms of water content, carbon content and phosphorus is not suprising. These two adjacent habitats are quite different even in visual inspection. While ST1 was a dry exposed rocky slope with red soil whereas the adjacent population occurs on a sheltered environment with *Helychrysum* bushes acting as shelters and maintaining the habitat moist and probably nutrient richer due to foliage litter. The soil in this habitat is black. Although the soil sample size is not large enough to draw concrete

scientific conclusions, they can be used as an indicator.

The two habitats are fairly well protected from fire hazards which have particular ramifications for Drakensberg mountain range with its history of fire regimes. Although there is no clarity about this pattern it is known that some areas are subjected to biannual fire regimes and others to annual fire regimes. However it is doubtful that the variation in *Festuca caprina* may be explained in terms of these fire patterns as there are differences between populations that were subjected to the same fire treatment as well e.g. N2S and N2B. Since there is no correlation between the population variability and environmental differences (see table x), these may be explained by the chance occurrence of genotypes with characteristics that are suited for the same environment. It is possible for small genetic differences between groups of individuals to become relatively large differences in some character measured at the population level (Wade and McCauley, 1980), due to interactions among individuals.

The present results are based on adult plants, whereas selection must act on the seedlings during the initial stages of the population establishment (Molgaard, 1986). No seedlings were observed in this study. These different genotypes may give rise to genetic incompatibility which may explain the lack of intermediates between the different populations. Each of the genotypes would be selected for its own character suite, meaning that the intermediates may be ill adapted for either of the environments. This means that they would be excluded from the

respective population habitats by natural selection.

5.1.1. POPULATION DIVERGENCE IN *FESTUCA CAPRINA*

Local population divergence has been fairly well documented. The divergence has been linked to several causative factors e.g. sharp differences in bedrock or underlying soil type; evolution of tolerant morphotypes in response to sharply different to toxic soil levels etc.

Experimental studies have also been done to test the validity of these results. These have convincingly demonstrated that not only population divergence over short distances is a fact but also that it can occur over a relatively very short space of time (McNeilly and Antonovics, 1968; Snaydon and Davies, 1971). Simultaneously and perhaps sometimes as a secondary result of these studies it has also been shown that given enough selective pressure or intensity, gene flow between or amongst populations does not inhibit population divergence (McNeilly and Antonovics, 1968; Scheiner and Teeri, 1987).

In other words the effects of gene flow between closely adjacent populations will only be manifested if there is not enough selective pressure to dictate population divergence and the direction towards that divergence. Thus population divergence between closely adjacent populations is made possible by natural selection which acts on these populations in exactly the same way as it does on populations distant from each other, resulting in reproductive isolation. Thus very large distances between popula-

tions are not necessarily a prerequisite for reproductive isolation. On the other hand large distances between populations does not necessarily lead to reproductive isolation and therefore population divergence.

Population divergence between local adjacent populations results from disruptive selection due to its high intensity. One example of disruptive population divergence is between adjacent populations in different but closely adjacent habitats. In this case habitat selection would be a factor that results in broadened conditions for polymorphism (Hedrick, 1986)

In *F. caprina* none of the above conditions exists in the closely adjacent populations. As has been shown earlier there are no significant soil differences between these populations, no habitat differences and no ecological differences. The only possibility left to explore is the chance occurrence of different genotypes otherwise known as mutation or genetic drift.

One of the possible causes of divergence in *F. caprina* populations is the mechanism of frequency -dependent selection. According to Dewald et al. (1964), this selection will automatically maintain polymorphism and also homozygosity within populations. In this way a restricted gene flow is not needed to explain a stable polymorphism with homozygotes. Polymorphism itself may be vital for protection of the plant population against grazing or veld fires and hence part of the driving force in its evolution.

It may be speculated that the differences between the populations

may be a consequence of a combination of phenotypic plasticity and genotypic differences. But the genotypic variability is clearly not due to diversifying selection, also known as the niche-variation hypothesis, i.e different alleles selected for different environments.

This study suggests that genotypically *F. caprina* Nees is sensitive to change through chance occurrence of new genotypes. If this is true the natural populations of *F. caprina* represent a rich source of genetic variation.

5.1.2. NOTES ON THE ANATOMICAL VARIATION

Comparative leaf anatomy in grasses has been used since 1931 (Dahlgren et al., 1985) as an aid in classification. Several principles regarding the use of this source of evidence have been established. One of them is that anatomical characters tend to be useful in classification at higher levels and are less useful when working below the generic level (Metcalfe, 1950; Lawrence, 1951). This study confirms this hypothesis.

Anatomical characters can be good predictors of a plant's physiological functions (Grundbacher, 1963). This may explain why the awns of barley, wheat, rye and oats are anatomically similar, (Grundbacher, 1963). On the basis of leaf anatomical attributes studied together with embryo structure and cytology, Decker (1964) reduced the number of genera in the festucoid group from 135 to 55. Studies of morphological attributes and chromosome races substantiate the observation that transverse leaf sections are a convenient way of summarising taxa under study (Borril,

1972).

It has been shown that the leaf cross sections in the narrow leaved fescues are species specific (Aiken et al, 1985; Linder, 1986) although sometimes they exhibit a large degree of overlap in their measurement values (Aiken et al, 1985). These characters can be used with a fair degree of accuracy for identification at specific rank, especially if the geographical origin and habitat are known (Aiken et al, 1985). At species level it seems that leaf anatomical characters can be correlated with their habitats. This is also true at infra-specific level where, in some cases, the anatomical characters can be used to separate any two populations from different habitats e.g. in *Festuca rubra,* (Dube & Morriset, 1987) and other species (Dubcosky and Martinez, 1988; Ellis, 1988). The characters used for this purpose include the greatest half length of the leaf cross section and the width of the midrib and type of micro-hairs, sclerenchyma distribution etc. Different species from different ecological regions, for example, show different amounts and distribution of sclerenchyma. An example of sclerenchyma tissue in *Festuca* species as an indicator of differences in habitats is provided by the wide spread species of this genus from mesic to dry and cold climatic conditions (Dubcosky and Martinez, 1988). This distribution is reflected both in reduced amount of sclerenchyma tissue and by a similar decrease in leaf size (Dubcosky and Martinez, 1988).

The leaf blades of the narrow leaved species have been studied extensively using the following characters: number of vascular bundles and adaxial ribs, the distribution of sclerenchyma and

the presence or absence of hairs and prickles, (Metcalfe, 1960; Aiken et al, 1985; Ellis, 1985; 1988). According to Metcalfe (1960) there is reason to believe that these characters vary to some extent within species in this group. However, even in other groups, discontinuities may not be clear between groups within a genus (Ellis, 1988). Although the differences may not reflect discrete entities, they may reflect evolutionary trends within a genus or species (Ellis, 1988). But while anatomical characters in the genus *Festuca* have been used for close to a century (Aiken et al, 1984), their usefulness should not be over emphasised, as they can be influenced by the environment in a more or less predictable way, much like macro-morphological characters (Davis 1983; 1988).

Anatomical characters therefore are not more or less conservative than morphological characters. Other characters that have been used to distinguish between taxa include the degree of openness of the panicle, number and size of the spikelets and also the extent of the sclerenchyma tissue.

Anatomical characters have also been used in conjunction with evidence from other sources, namely, chromosome numbers and morphological characters (Frederiksen, 1977) to delimit taxa. Suites of anatomical characters, for example, differences in mesophyll and micro-hair shape, can also be used to distinguish species groups (Gibbs Russell and Ellis,

1987). Dubious plants have been placed in their respective taxa using leaf anatomical characters from the cross sections (Ellis,

1986).

The anatomy of this species is typical of the narrow leaved fescues (Aiken et al, 1985; Linder, 1986), in certain attributes, such as narrow outline of the cross section, the presence of deep and narrow ribs and furrows, reduced sclerenchyma and distribution of sclerenchyma. However, a combination of certain characters distinguishes this species from other fescues. These characters include, the number of ribs and distribution of sclerenchyma. The ribs vary from 5 to 7 while the sclerenchyma is adjacent to the abaxial epidermis and restricted below each vascular bundle (Fig. 19a -b).

One exception was observed where the sclerenchyma was also found in the inside of the vascular bundles adjacent to the adaxial epidermal cells (Fig. 19c). This variation was first recorded by Linder (1986). I suggest that the specimens with this kind of vascularisation represent hybrids between *F. caprina* and *F. humidicola,* a new species found growing together with these plants. These hybrids would be similar to *F. caprina* in external appearance.
Although the measurement values differ between plants, the leaf anatomy tends to remain stable.

5.1.3. Population distribution, habitat and variability

In South Africa *Festuca caprina* is a widespread species ranging from the eastern Cape to the Eastern Transvaal. According to Killick (1978) this area is designated the Drakensberg, and is composed of an archipelago of mountain islands. In this area, *F.*

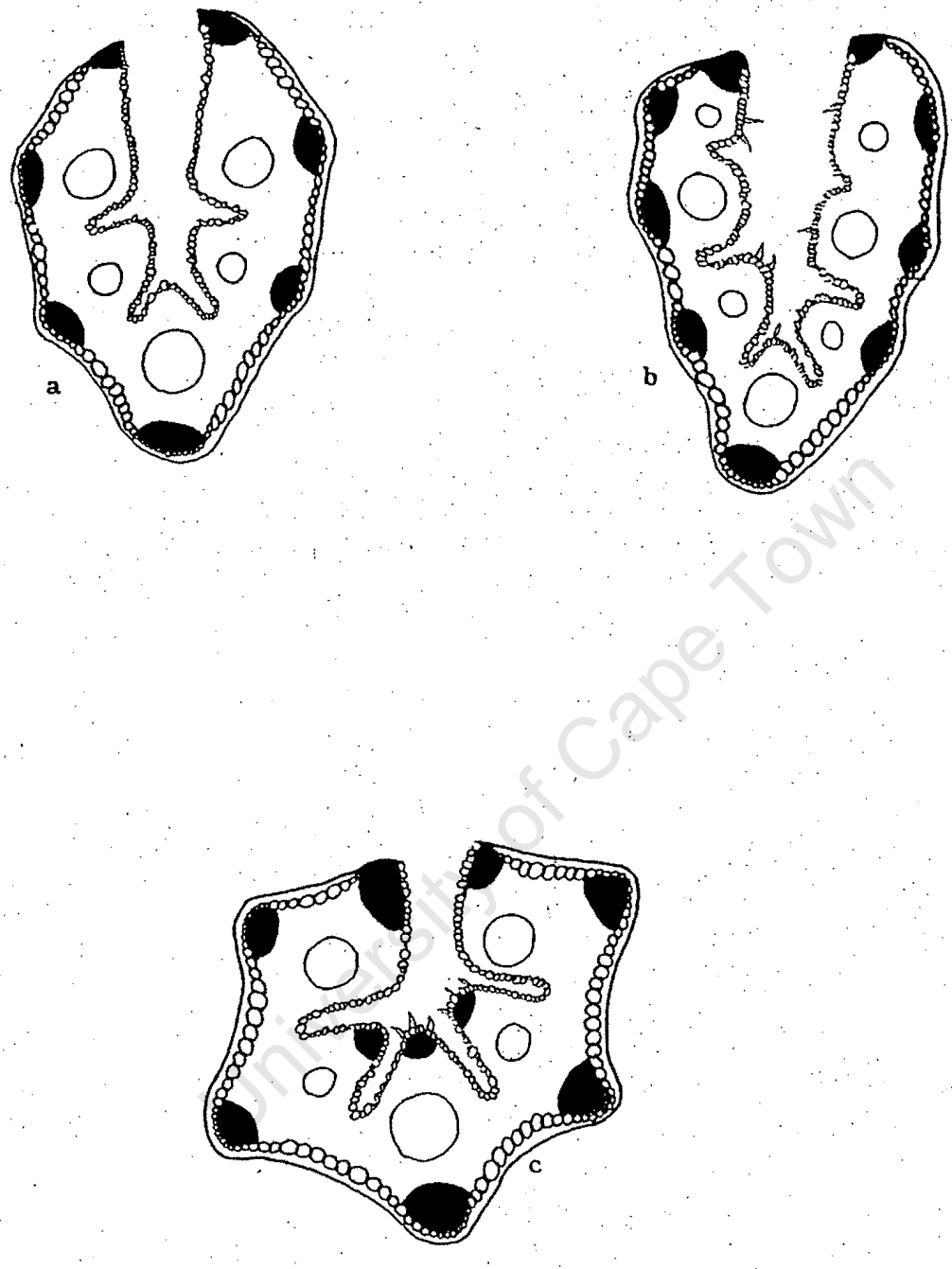


Fig. 19. Camera lucida drawings showing variation in leaf cross sections of Festuca caprina.
Voucher specimens: a) Sokutu 111 (BOL), b) Sokutu 119 (BOL), c) Sokutu 116 (BOL).

caprina is represented by a number of striking, morphologically diverse populations. This morphological diversity does not represent geographical variability nor habitat differences.

The different morphotypes can best be seen in the centre of the Drakensberg mountain range. In this area a number of morphological variants may be found without any geographical groupings. This is evident in that more than two populations representing different morphotypes may be found in the same area. In other cases the distance between two populations is less than 1m. Each population in turn is exceedingly uniform. There is no apparent evidence of genetic interchange between any two adjacent populations. This is witnessed by the lack of continuity between locally adjacent populations.

The distance between any two populations does not seem to affect the distinctness of the populations. In most cases the populations are subjected to homogeneous environmental constraints. The populations differ from each other mostly in vegetative morphology, viz: plant size growth form and to a lesser extent foliage colour. There is a limited variability in the inflorescence and that is in the degree of openness and the arrangement of the spikelets or spikelet branches on the rachis.

Plants are usually erect, loose or dense tufts up to 1,3m high. The inflorescences are usually well exserted from the leaves such that the longer the leaves, the longer the culms. Some populations have plants that are bigger at base forming very big tussocks. This may be a response to grazing (Ellis, 1988) or

possibly to fire hazards. The culms are usually erect and slender, the number of which varies with the tussock size from one to several. They are usually about twice the length of the leaves.

The leaves are basal, pale green to bright and dark green, always folded, usually smooth sometimes scabrid on abaxial surface; smooth, scabrid to puberulous on the adaxial surface. All the populations studied have filiform leaves. In this respect the Southern African plants differ from the East tropical African in that the latter sometimes have flat leaves (Clayton, 1970). In those plants in which the inflorescence is dense, closed and compact they droop to one side. This is probably due to that the culms are slender and the weight of the inflorescence pulls the rachis downwards. When the inflorescence is loose and open spikelets are borne on relatively long branches and pedicels. In these cases the inflorescence is always upright. The population variation does not reflect any geographical groupings. Different morphological groups occur on homogeneous habitats where plants are subjected to the same environmental conditions. This variation pattern suggests that genetic differences exist between different populations of this species.

5.2. CONCLUSIONS

The results of this study show that *Festuca caprina* Nees is a very variable species. However, it is also clear that the variability of structures overlap from one population to another. A striking feature of the variation pattern is the significant degree of population differentiation within one locality. The variation pattern is not correlated to the geographical distribution. At least within one locality (ST1 and ST2) the microhabitats seem to influence the variation pattern.

Based on these results and also on field observations there is not enough justification for the recognition of infra-specific taxa in *F. caprina*. The characters on which these taxa are delimited, i.e. lemma hairiness, awn length and leaf indumentum seem to be variable. Another character used i.e. the rigidity of the leaves also does not seem to hold as it is very difficult to quantify its variation. Therefore it was not used in this study. Thus the evidence to delineate these taxa is so far not convincing. I suggest that recognition of infra-specific taxa in this species would be undermining its biological nature. As already suggested by other taxonomists (Clayton, 1971; Ross, 1973) it is accepted that *F. caprina* is a polymorphic species.

It is also clear from this study that the anatomical characters are not significant in delimiting taxa below the species level in *F. caprina*. This agrees with Aiken et al (1985) who showed that these characters are not important below specific level in *Festuca* in general. This study also shows that the reproductive char-

acters are the least variable characters.

Of all the variation in this species most variability occurs within one locality. This implies that if within a locality one representative would be sampled for study, a substantial fraction of variants would remain undetected.

The scope of this study did not allow further investigations to the nature of the genotypic variability. Future research should explore this field.

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II. A NEW SPECIES IN THE GENUS *FESTUCA L.*

TABLE OF CONTENTS

ABSTRACT

Festuca humidicola Sokutu, a species of *Poaceae* from the Drakensberg is described and illustrated morphologically and anatomically. This species is closely related to *F. caprina* Nees from which it differs in a few characters. Some of the characters include: a rhizomatous root system, an expanded, v-shaped leaf blade, and fewer florets.

ACKNOWLEDGEMENTS

I would like to thank my project adviser, Dr. P. Linder for his assistance throughout this project. I am indebted to Dr. J. Rourke for the Latin translation. Miss B. Laurens provided the morphological illustrations. This project was done while holding a Foundation for Research Development studentship at the University of Cape Town.

I am grateful to my family and Nosisi for their love and encouragement throughout my studies.

Lastly, to my wife Nosisi, whose support, love, and tolerance were invaluable while I was away from home, I dedicate this project.

INTRODUCTION

F. humidicola Sokutu is the tenth member of the South African fescues. Its closest relative *F. caprina* Nees is distinguished from Southern African species of this genus by possessing permanently folded leaves (Nees, 1841; Clayton, 1970; Chippindall, 1955), together with a combination of other characters including anatomical characters.

Hilliard and Burt (1986) reported the occurrence of a distinct undescribed species on the Drakensberg, which they related to *F. caprina* Nees. The broad leaves and rhizome, however, suggested that it was a distinct species. After close examination other unique characters were discovered.

Materials and Methods

Morphology

Specimens of this new species were collected from three populations: one in Organ Pipes and two in Witzieshoek. Spikelets and pieces of leaves, about 5cm long were fixed and preserved in F.A.A. (20 Alcohol (50%): 1:Acetic Acid: 1:Formalin) immediately after being picked. Spikelet morphological measurements were taken in the laboratory under a dissecting microscope at variable magnifications depending on size.

Leaf Anatomy

Fresh material from about the middle of each leaf from six leaves, two from each population, was fixed and stored in F.A.A. indefinitely. Leaves that were visibly unhealthy were avoided for the study. For immediate data recording and examination, temporary mounts were made: leaf cross sections were obtained by using two types of freezing stage microtomes; namely Carbon dioxide microtome and an electrical microtome. Staining was done with toluidine blue. A section, 20 microns from one leaf per plant was made.

The sections were examined immediately under a dissecting microscope at 50X. Notes on the following were taken: i) thickness of the midrib, ii) number of large vascular bundles, iii) number of small vascular bundles, iv) number of ribs; v) thickness of sclerenchyma at midrib region, vi) distribution of the sclerenchyma and variability in the shape of the cross sections were taken.

For permanent mounts the material preserved in F.A.A. was removed and desilicified in 80% Hydroflouric acid for twelve hours (Breakwell, 1914). After rinsing in water for about one hour they were subjected to a dehydration process using a Sakura tissue processor (Fisher scientific) as follows: two changes of eight hours each in:

i) 70% alcohol

ii) 100% alcohol

iii) n - Propanol

iv) n - butanol.

This method is a modified version of that of Feder and O'Brien (1968). After dehydration the pieces of leaves were embedded after soaking in two changes of melted pure wax (Paraplast+) for twenty-four hours each. Cross sections about 15-20 microns were obtained using a slide microtome. The leaf cross sections were double stained by using Saffranin and Fast Green (Johansen, 1940). They were then mounted permanently in DPX. Camera lucida drawings were made the cross sections. The epidermal scrapes were made by using the manual scrapping method of Metcalfe (1960).
In the leaf anatomical descriptions the terminology of Ellis (1976; 1979) is used.

DESCRIPTION

Morphology

Plantae laxae vel densae caespitosae, rhizomatosae. Foliorum laminae expansae, anguste v-formatae, glabrae, scaberulae, 9 - 12 costis. Ligula ad 0.5 mm longa, glabra, integra. Inflorescentia contracta vel aperta. Spiculae oblongae, atroviride, interdum purpureo-varigatae, glabrae, 2-4 floribus. Glumae conspicue inaequales; gluma inferna anguste lanceolata ad ovata, 1-nervata, 3.5 - 4.5 mm longa; gluma superna lanceolata ad late ovata, 4 - 5.5 mm longa. Arista 1.5 - 2 mm longa.

TYPUS: Natal: Cathedral Peak (Organ Pipes), near stream, 2750 m a.s.l. Sokutu (BOL 117 Holotypus !).

Plants perennial, densely or loosely caespitose, rhizomatous. **Culms** slender, erect or curved at base, 150 -- 350mm high, simple with one or two basal nodes; surface ribbed; upper half of apical internode exposed. **Leaves** mostly basal; sheath tightly rolled on culms, glabrous to scaberulous, blades expanded, narrowly v-shaped in cross section, glabrous - scaberulous, up to 250mm long, 1.5 -- 3mm wide; ligule a membrane, entire or slightly cilliate, up to 0.5mm long. **Inflorescence** narrowly open, 60 -- 100mm, ovate, 5 - 10 nodes; rachis glabrous or scaberulous; branches filiform, alternate. **Pedicels** conspicuous, gradually thickened, glabrous or scabrid. **Spikelets** numerous, obovate - oblong, 2 - 4 flowered, pale to bright green, sometimes with a tinge of purple, 5 -- 9mm long. **Glumes** conspicuously unequal, the lower narrowly lanceolate to ovate, 1 - nerved, 3.5 -- 4.5mm, upper lanceolate to broadly ovate, 3- nerved, 4 -- 5.5mm, dark green, purple variegated. **Lemma** glabrous to scabrid, broadly ovate, apex 2- fid, 4 -- 6mm long, nerves almost invisible, middle nerve excurrent into a short awn. **Awn** 1.5 -- 2mm long. **Rachilla** scabrid to puberulous, 0.5 -- 1mm long. **Palea** as long as the lemma. **Lodicule** membranous, one or two lobed, up to 0.5mm long. **Ovary** obovate, hairy on top. Anthers 3, 0.3 - 1mm long. **Stigma** plumose. **Caryopsis** broadly obovate, convex on dorsal side, linear on ventral side when fresh, ventrally sulcate when dry; embryo obovate, less than 1/4 of the full size of the fruit; hilum linear, about 3/4 the full size of the fruit or as long as the full size; coat sculpturing irregular. (See figures 1-10 for illustrations).

Figs. 1 – 10. Morphology of Festuca humidicola.

KEY TO FIGURES 1-10. Drawings showing the morphology of F. humidicola (Sokutu 117 BOL)

1 = Whole Plant (X1)

2 = Ligule (X12)

3 = Spikelet (X15)

4 = Upper and Lower glumes (X15)

5 = Lemma, ventral side (X12)

6 = Seed with remains of ovary, ventral side (X20)

7 = Seed with remains of ovary, dorsal side (X20)

8 = Palea, ventral side (X15)

9 = ovary with stigmata and ovary on top (X40)

10= Lodicule (X50)

Leaf Anatomy

Leaf outline: Broad, flat to wide, horizontally elongated to narrow and vertically elongated. **Ribs and furrows:** medium, adaxial ribs almost all rounded, furrows deep and narrow, sometimes cleft-like, ribs and furrows sometimes not developed. **Median vascular bundle:** not distinct from lateral vascular bundles. **Vascular bundle arrangement:** no regular pattern, variable in number from 9 - 12; three first order vascular bundles: one median, two lateral; one on either side; 2 -3 second order vascular bundles between the median first order vascular and the lateral first order vascular bundle on each side. All vascular bundles situated in the centre of the leaf cross section.

Vascular bundle structure: round to ovate in shape; phloem

adjoins the inner bundle sheath; metaxylem cells big and distinct, 3 - 4; xylem and phloem distinct. **Vascular bundle sheaths:** double; outer sheath cells parenchymatous, isodiametric, lack chloroplasts, thin walled, bigger than mesophyll cells; inner bundle sheath cells smaller, irregularly thickened, radially and tangentially lignified. **Sclerenchyma:** reduced, interrupted, adjacent to adaxial and abaxial epidermis, opposite each vascular bundle on the inner and the outer side, sometimes attached to the first order vascular bundle on the outer side, never attached to the second order vascular bundle, sclerenchyma caps at margins.

Mesophyll: cells irregular, tending towards radiate condition, lateral cell count more than 4, continuous between bundles, no arm cells or fusoids, air spaces not frequent. **Epidermis:** adaxial epidermal cells very small, no cuticle, bulliform cells distinct, medium size, at base of furrows; prickles absent to few; abaxial epidermal cells bigger, bulliform cells absent, cuticle very thin, prickles absent to few. (see Fig. 11)

Abaxial epidermis, surface view:

Intercostal long cells elongate, rectangular, relatively wide, walls straight or sinuous. Cell shape and size variable within and between individual intercostal zones, sometimes fairly consistent across individual intercostal zones; long cells usually bigger at the middle of the intercostal zones, decreasing towards the sides; long cells adjoin one another, or separated by a silica cell and a cork cell. Silica and cork cells very short,

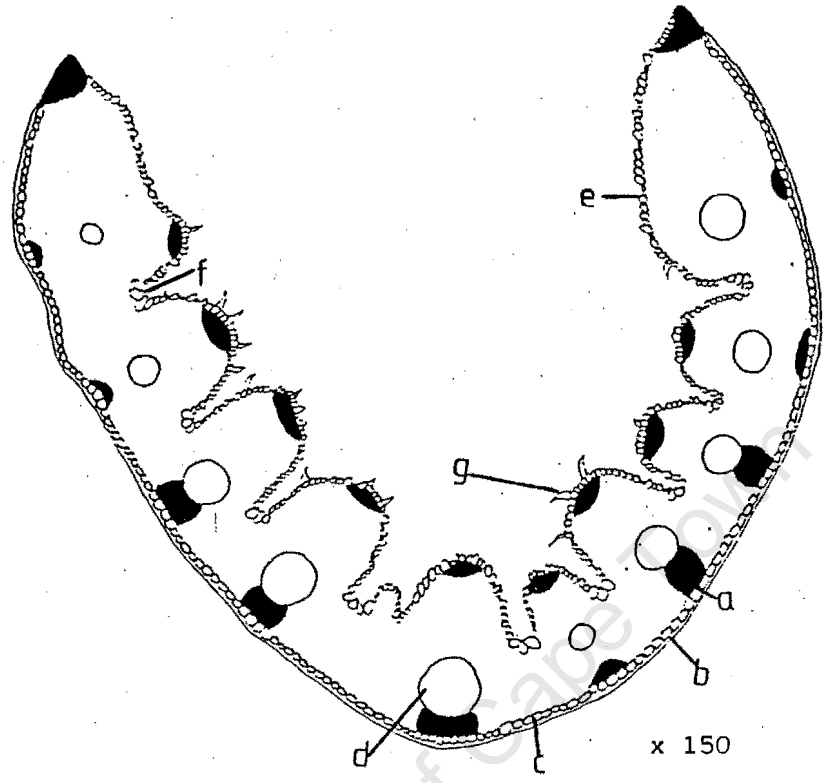

Fig.11. Camera lucida drawing showing a leaf cross section of Festuca humiducola, Sokutu 117, Bol

a = Sclerenchyma

b = cuticle

c = Abaxial epidermis

d = Median vascular bundle

e = Adaxial epidermis

f = Bulliform cells

g = Prickles

dome shaped, adjoined to one another. No bulliform cells nor stomata on this surface view.

Adaxial epidermis, surface view:

Costal and intercostal zones distinct. Walls of the intercostal long cells straight. Stomata interspersed among the long cells, irregularly arranged; more or less rectangular or dome shaped, subsidiary cells almost parallel, guard cells situated at each end; long cells straight walled; no short cells.

Ecology

This species has a very narrow ecological niche. It grows in wet areas, sometimes near streams.It has been observed only on soil that appears black at about 2050 - 2750m a.s.l. Only three populations were seen, one in Organ Pipes and the other two in Wietzieshoek (see Fig. 12). This species appears to be flowering from December to February.

DISCUSSION

F. humidicola is near *F. caprina* in both morphological and anatomical characteristics. However, certain combinations of both characters distinguish between these species (see table 1.). *F. humidicola* grows sympatrically with *F. caprina* but the former prefers wet or moist habitats. Although F. caprina also occurs in wet habitats it is not restricted to them. Some characteristics of *F. humidicola* can be correlated to its habitats, e.g. the open

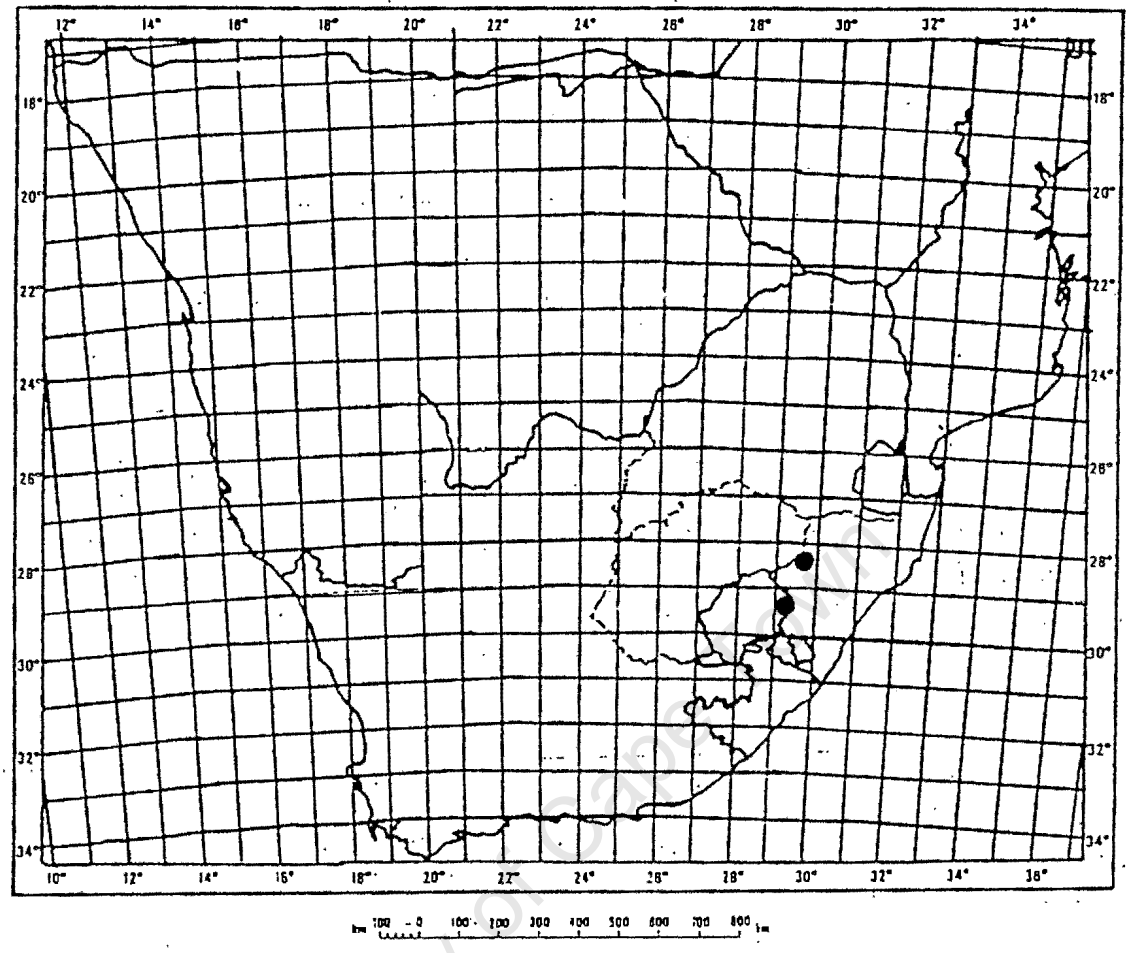

Fig. 12. Known geographical distribution of Festuca humidicola in southern Africa.

leaf blade, the extent and the distribution of the sclerenchyma, the frequency of the stomata.

It may be speculated that *F. humidicola* is a derivative of *F. caprina*. It is possible that this species interbreeds with some genotypes of *F. caprina* and that the hybrid is identical to the latter. This is surpported by the fact that only one sample from the *F. caprina* populations was found to have sclerenchyma forming caps on the inside of the vascular bundles adjacent to the adaxial epidermis. Members of these two populations grow together forming almost one population.

When dry this species is not easily distinguished from *F. caprina*. The leaves tend to roll inwards and the rhizome is not always so distinct depending on the way in which the plant was uprooted. At close examination, however, it can be observed that the spikelets are shorter due to fewer florets.

Similarities and dissimilarities with *Festuca caprina*

F. humidicola is different from *F. caprina* in its general appearance and in its broad leaves and rhizomatous root system. *F. humidicola* appears to have fewer spikelets than *F. caprina*. Another unique feature of *F. humidicola* is the reduction in the number of florets from 3 to 9 in *F. caprina* to 2 to 4 in the former. The panicle resembles that of *F. caprina* in its structure.

Table 1: Similarities and dissimilarities between *F. humidicola* and *F. caprina*.

	F. caprina	F. humidicola
Root system	Fibrous	Rhizomatous
Growth form	Perennial	Same
Number of nodes	Two - three	Same
Leaf blade	Filiform	Open
Leaf indumentum	Glabrous/scaberulous	Same
Inflorescence	Open or closed	Same
Spikelet length	6.5 - 14.5mm	5 - 9mm
Number of florets	3 - 9	2 - 4
Leaf cross section	narrow	Broad - wide
Furrows	Deep and elongated	more elongated
Number of ribs	5 - 7	9 - 12
Bulliform cells	not distinct	usually distinct
Bundle sheaths	double	same
Mesophyll	irregular	same
Distribution of Sclerenchyma	Abaxial	Ad- & abaxial
Frequency of stomata	infrequent	frequent
Abaxial epidermal cells	small	very small
Cuticle thickness	thicker	thin
Caryopsis	same	same

Population Variability

The three populations that have been observed vary in plant size. However it was difficult to determine whether this variability is related to the age of the plants or not. The leaf length seemed

to vary with the culm length: the longer the culm the longer the leaves and vice versa. In two of the populations the inflorescences were closed and open in the other one.

The leaf cross sections revealed that the presence of sclerenchyma caps on the inside of ribs is not consistent. Sometimes the sclerenchyma caps are lacking. This may be related to the age of a plant and the stage of leaf development.

Conclusions

Although *F. humidicola* is closely related to *F. caprina* it is demonstrably distinct from it and other species of the genus *Festuca*. It is restricted to wet areas. This makes it a good example of sympatric speciation where long distance is not a prerequisite for speciation.

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