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Panicum simulans (Paniceae, Poaceae), a new species from southern Africa and its leaf anatomy

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ABSTRACT

Panicum **simulans** Smook from northern Namibia is formally described. The morphology and leaf blade anatomy in transection and surface view, as observed under the light microscope, are described. The species is compared to others with which it has been confused in the past. *P.* **simulans** can be readily distinguished from *P. novemnerve* Stapf and *P. schinzii* Hack. on the basis of both anatomical and morphological characters such as the venation of the lower glume and the photosynthetic anatomy, which is of the NAD-me subtype of the C_4 photosynthetic pathway. On this basis it appears that *P.* **simulans** is closely allied to the *P. coloratum* L. group of species and should be placed in section *Panicum* of subgenus *Panicum*.

UITTREKSEL

Panicum **simulans** Smook vanaf die noordelike Namibië word formeel beskryf. Die morfologie en blaaranatomie, in deursnee- en oppervlakaansig, soos met die ligmikroskoop waargeneem, word beskryf. Die morfologie en blaaranatomie van *P.* **simulans** word vergelyk met dié van twee ander spesies wat verwarring in die verlede geskep het. *P.* **simulans** kan maklik van *P. novemnerve* Stapf en *P. schinzii* Hack. onderskei word op grond van die bearing van die onderste gluma en die fotosintetiese anatomie wat van die NAD-me subtipe van die C_4-fotosintetiese weg is. Op grond van hierdie gegewens word *P.* **simulans** in die seksie *Panicum* van subgenus *Panicum* geplaas.

Panicum simulans Smook, sp. nov.

Panicum sp. 2 (*Giess 8605*) in Gibbs Russell *et al.*: 242 (1990).

Panicum spp. in Group 3a in Ellis (1988).

Panicum simulans Smook, sp. nov., *P. novemnervi* Stapf similis sed gluma inferiori uninervi, flosculo inferiori masculo, paleaque inferiori bene evoluta differt; *P. schinzii* Hack. similis sed nodis culmorum adpresso-hirsutis, apicibus glumae superioris et lemmae inferioris erectis vel recurvis, atque chloroplastis centripetis, non centrifugis, differt.

Annual. Plant variable; usually yellowish green in colour, often flushed purple. *Culms* erect to geniculate, 600(−1 200) mm high (from plant base to top of inflorescence); sometimes rooting at nodes; nodes with adpressed silvery white hairs pointing upwards; *base* covered with leaf sheaths; internodes usually not visible. *Leaf sheaths* glabrous or with bulbous-based hairs varying in length and size of hair and relative size of base. *Ligule* a fringed membrane 1.4 mm long (membranous rim 0.3 mm, cilia 1.1 mm long). *Leaf blade* linear, 5−200(−250) × 2−15 mm, straight or cordate at base, flat, many-nerved, bulbous-based hairs present or absent; apex acute to acuminate; margins white, smooth to scaberulous to densely scabrid; adaxial surface densely papillate especially on lower leaves; nerves of abaxial leaf surface smooth, occasionally densely scabrid especially near leaf apex (variable on same plant).

Inflorescence a panicle (80−)160−250(−400) mm long, narrowly obovate to obovate, occasionally oblanceolate, sometimes asymmetrical (lowest branch longest, protruding beyond other branches), moderately branched, usually ascending and spreading; lowest branches single or a number arising from same side, not whorled; next set of branches often whorled or in a pseudo-whorl; branches naked for a long way up from base with spikelets crowded at apices, smaller branches usually scabrid with prickles becoming denser, longer and larger towards spikelets; spikelets usually in pairs on long-short pedicels on branchlets. *Spikelets* narrowly obovate to obovate-elliptic, (2.2−)2.4−2.6(−3.0) mm long, acute to acuminate, often flushed purple. *Lower glume* broadly ovate, $^1/_3$ to just over $^1/_2$ as long as intact spikelet, clasping base of spikelet, membranous; central nerve distinct, often scaberulous to scabrid; lateral nerves obscure, if present, only visible at base; apex acute to acuminate, sometimes minutely mucronate or with a brush of prickles. *Rachilla* pronounced between glumes. *Upper glume* 2.4−2.6(−3.0) mm long, longer than lower lemma, membranous, 7−9(11)-nerved (nerves nearest margins sometimes obscure and short); central nerve thickened at apex, forming a usually scabrid mucro; apex acute to acuminate, either erect or slightly recurved outwards; margins below apex membranous and folding inwards, often flushed purple and then mainly at apex. *Lower floret* male only; anthers 3, developed 1.4−1.7 mm long or rudimentary, both conditions present on same inflorescence, dark orange-brown. *Lower lemma* similar to, but shorter than upper glume, fitting into its apex, (7−)9-nerved; cross venation often visible; central nerve scaberulous, thickened towards apex; apex acute to truncate; margins broad and membranous, either folded in or out, often purple especially near apex. *Lower palea* well developed, nearly as long and as wide as lower lemma. *Upper lemma and palea* smooth, shiny, pale, white to straw-coloured, occasionally dark with

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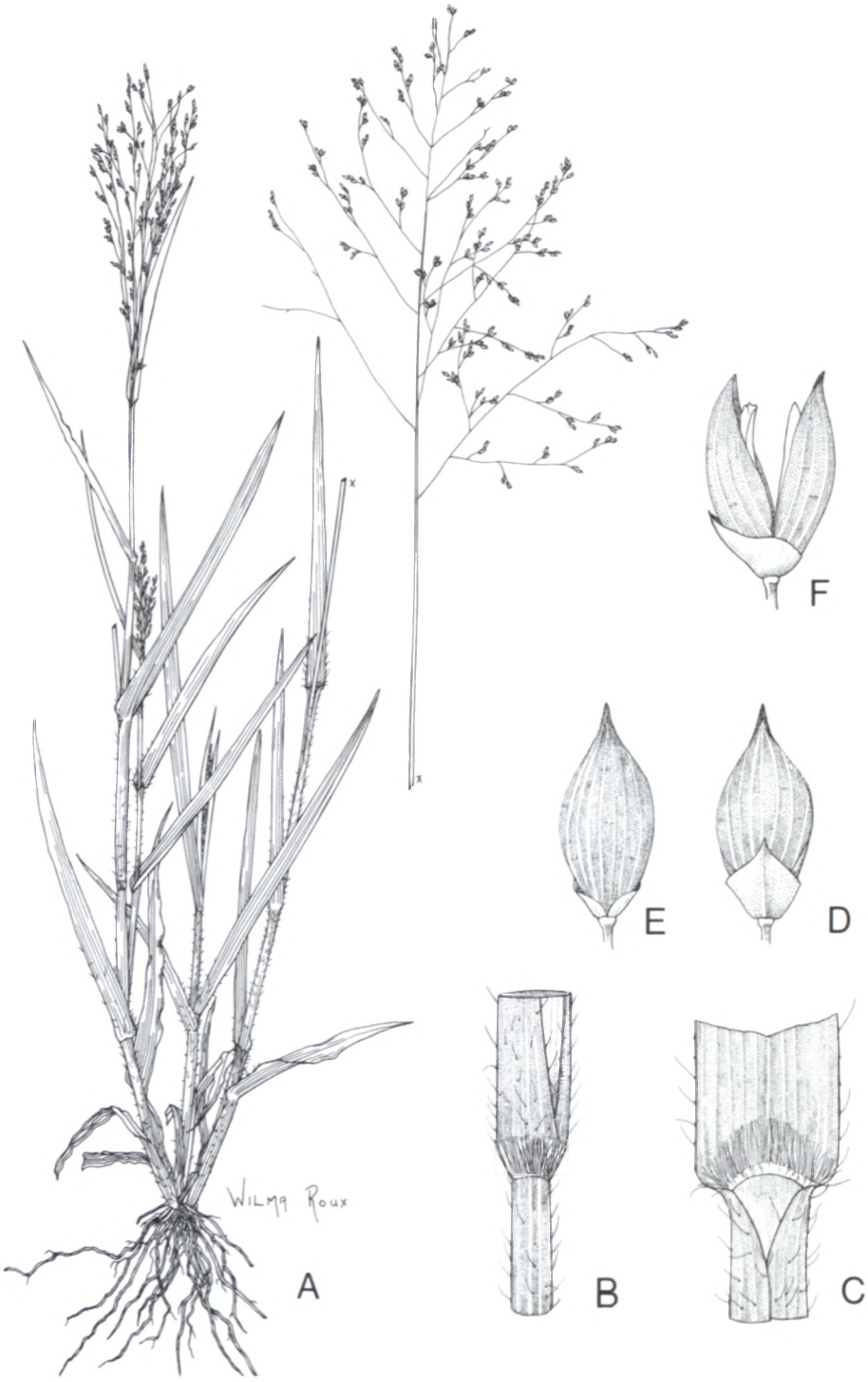

FIGURE 1.—*Panicum simulans*. A, habit, × 0.5; B, node showing adpressed hairs, × 2.5; C, ligule, × 2.5; D, spikelet showing lower glume, × 10; E, spikelet showing upper glume, × 10; F, lateral view of open spikelet, × 10. From *Smook 5108* and *Giess 8605*.

distinct yellow nerves on upper lemma, both colour forms sometimes present on same plant. *Styles* 2, separate; stigmas plumose, purple to dark brown (on herbarium specimens). Figure 1.

TYPE.—Namibia, 1915 (Otjihorongo): 25 km N of Outjo on road to Okaukuejo, (−DD), *Smook 5108* (PRE, holo.) (*Smook 5108a*, PRE, isotype*).

Panicum simulans has been confused with *P. schinzii* Hack. and *P. novemnerve* Stapf in the past, and the specimens now included in this new species have been misidentified as either of these two species. However, this study shows that several characters serve to separate these three species clearly and to justify the recognition of *P. simulans* (Table 1). The specific epithet refers to the superficial similarity between *P. simulans*, *P. schinzii* and *P. novemnerve*.

Figure 2 shows the known distribution of *P. simulans*. It is restricted to northern Namibia but may possibly also occur in southern Angola. It is associated with various vegetation types ranging from mopane woodland to mopane mixed with *Acacia*, *Combretum* or *Terminalia* to sweet grassland on limestone soils such as occur around Etosha Pan.

Panicum simulans is hydrophytic and grows typically in areas with seasonally high moisture regimes as found in vleis and around fountains. It may even occur in more

* This is the anatomical voucher specimen.

TABLE 1.—Comparison between *Panicum novemnerve*, *P. simulans* and *P. schinzii*

	novemnerve	*simulans*	*schinzii*
culm nodes	adpressed hairy	adpressed hairy	glabrous
lower glume venation (distinct)	3–5-nerved	1-nerved	1-nerved
apex of upper glume and lower lemma	erect or recurved	erect or recurved	folded inwards
lower floret	sterile	male	male
lower palea	reduced	well developed	well developed
Kranz chloroplasts	centripetal	centripetal	centrifugal

ephemerally moist situations such as in depressions in disturbed situations along roadsides or irrigated lands or in natural hollows in granite outcrops or saturated soil pockets overlying calcrete.

Specimens examined

NAMIBIA.—1713 (Swartbooisdrift): Kaokoveld, (–DD), *Merxmueller & Giess 35538*. 1813 (Ohopoho): Kaokoveld, (–BB), *De Winter & Leistner 5160*. 1815 (Okahakana): Etosha National Game Park, (–DC), *Le Roux 1399*. 1817 (Tsintsabis): 56 km S of Namutoni on road to Tsumeb, (–CD), *Smook 5153**; Farm Falkenhain GR/TS 303, (–DA), *Giess 15090*. 1914 (Kamanjab): 15 km N of Otjovasandu, (–AB), *Giess 9253*; Farm Grootberg, (–CD), *Du Toit 236*. 1915 (Okaukuejo): Etosha National Game Park, Vogelnestvley, (–BB), *Giess & Mueller 13971*, 10 km S of Okaukuejo, *Giess & Loutit 14143*; 9 km E of Okaukuejo, *Smook 5109**, (–BB), *Tinley 1299A*; Ombika, (–BD), *Le Roux 328*; Ombika detour, *Giess & Loutit 14113*; near Ombika, *Giess 15078*; 25 km N of Outjo on road to Okaukuejo, (–DD), *Smook 5108**. 1916 (Gobaub): Etosha National Game Park, Olifantsbad, (–AA), *Ellis 5271**, *5273**; Gemsbokvlakte, (–AA), *Smook 5110**; Halali, (–BA), *Van der Westhuizen 23*. 1917 (Tsumeb): Tsumeb, (–BA), *Giess 8605*. 1918 (Grootfontein): Farm Sus, (–AB), *Schweickerdt 2144*. 2015 (Otjihorongo): Farm Pamela, (–AB), *Volk 2855*; Farm Babatsi, (–AB), *Gibbs Russell & Smook 5628**; Farm Straussenheim OUT 133, (–BB), *Giess, Volk & Bleissner 6004*. 2115 (Karibib): Farm Etemba, (–BC), *Giess 10799*; Farm Schlucht OM 162, (–DA), *Giess 8435*; Farm Ameib, *Giess, Volk & Bleissner 5898*, *De Winter & Hardy 8072*.

LEAF ANATOMY OF *PANICUM SIMULANS*

In order to obtain further evidence relating to the taxonomic status and position of *P. simulans*, a detailed anatomical study was undertaken. The methods used are described in Ellis (1988) and the terminology used is defined in Ellis (1976 & 1979). The following abbreviations will be used:

vb/s = vascular bundle(s)
1'vb/s = first-order vascular bundle(s)
2'vb/s = second-order vascular bundle(s)
3'vb/s = third-order vascular bundle(s)
ibs = inner or mestome sheath
obs = outer or parenchyma sheath

Leaf blade in transverse section

Outline: expanded blade, flat to very broadly V-shaped; arms of lamina straight or gently undulating; blade symmetrical about midrib. *Ribs and furrows*: shallow and wide adaxial furrows present between all vbs; slight, rounded ribs occur in association with all vbs; similar ribs occur over all vbs. No abaxial ribs or furrows present. *Median vascular bundle*: variable, either median bundle only present (this indistinguishable structurally from lateral 1'vbs and without additional parenchyma tissue) (Figure 3A) or keel with associated colourless parenchyma tissue present (Figure 3B); 1, 3 or 5 vbs incorporated in keel; all bundles abaxially located; larger keels rounded with single adaxial groove; no adaxial sclerenchyma developed and abaxial girders associated with all vbs; no air spaces in keel. *Vascular bundle arrangement*: 5, 7, 9 or 11 1'vbs in transection; 3, 4 or 5 3'vbs between consecutive 1'vbs; narrower leaves without keels, with 5 1'vbs and with three 3'vbs between successive larger bundles. No 2'vbs. All vbs situated in centre of blade. *Vascular bundle description*: 3'vbs circular in outline with xylem and phloem distinguishable. 1'vbs circular in shape, lysigenous cavities present (Figure 3E, F) and metaxylem vessels narrow (diameters less than those of obs cells) and circular. *Vascular bundle sheaths*: obs conspicuous, round, entire (except with small abaxial interruption in 1'vbs) and without extensions; consists of 6, 7 or 8 cells around 3'vbs and 11–14 cells around 1'vbs; obs cells fan-shaped with radial walls straight and outer tangential walls inflated (Figure 3E, F); all cells similar in size and shape; chloroplasts dense, filling entire cell lumen or concentrated centripetally, near inner tangential wall. Ibs absent in 3'vbs; complete but inconspicuous in 1'vbs; cells very much smaller than obs cells; adaxial cells slightly larger and thin-walled; lateral and abaxial cells uniformly thickened but degree of secondary thickening very variable. *Sclerenchyma*: minute adaxial and abaxial strands only associated with 1'vbs; no fibrous tissue in association with 3'vbs. Small sclerenchyma caps in leaf margin (Figure 3A). *Chlorenchyma*: distinctly radiate; single layer of tabular cells completely surrounds all vbs (except sometimes for a short abaxial interruption with 1'vbs); radiating chlorenchyma of successive bundles in direct contact and not separated by colourless parenchyma. No colourless parenchyma tissue present (except in midrib, if present). *Adaxial epidermal cells*: bulliform cells small, in rather extensive groups; central bulliform cell occupies less than $^1/_4$ of leaf thickness; cuticle very thin; no macrohairs, except rarely in association with margin; no prickles or hooks evident; cuticular papillae common, much narrower than epidermal cells and with one per cell as seen in

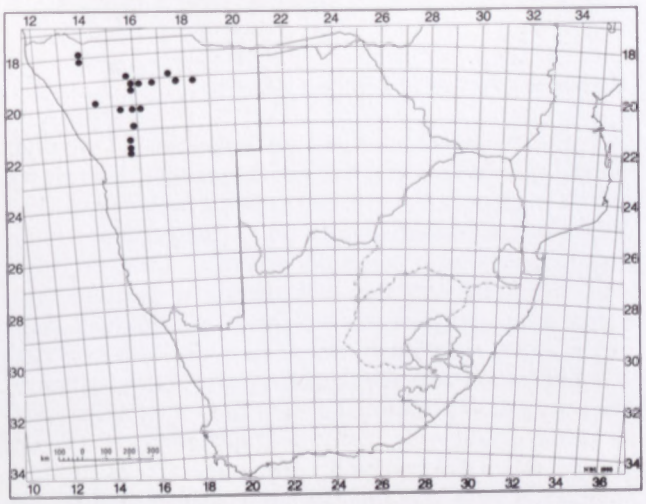

FIGURE 2.—The known distribution of *Panicum simulans*.

* voucher specimens for anatomical study.

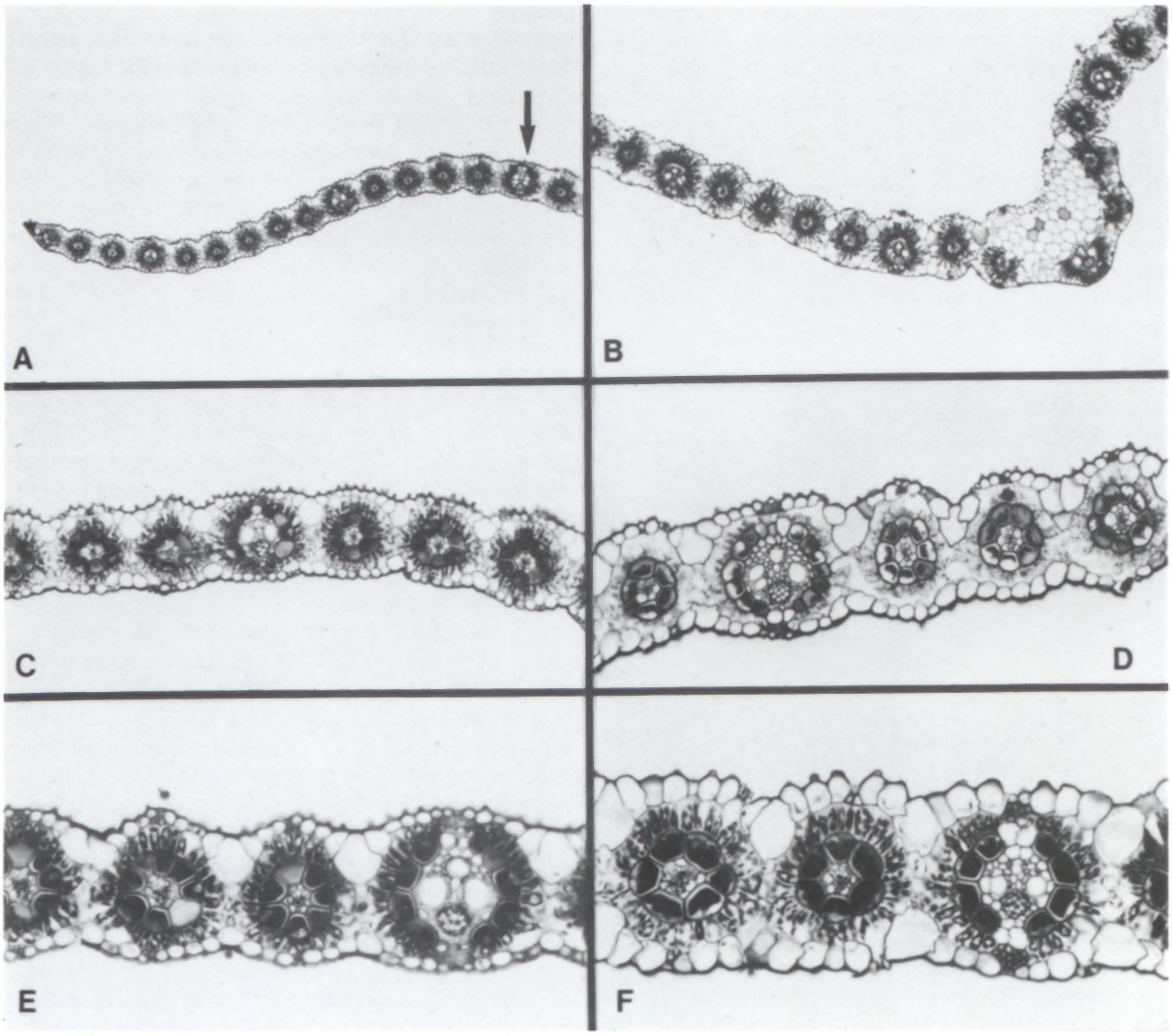

FIGURE 3.—Leaf blade anatomy of *Panicum simulans* as seen in transverse section. A, outline of specimen without keel; median vascular bundle only (arrowed), this bundle structurally indistinguishable from other first-order vascular bundles; B, outline of specimen with distinct keel incorporating four vascular bundles and adaxial colourless parenchyma tissue; C, typical C_4 photosynthetic anatomy with prominent parenchyma sheaths; D, specimen showing distinct centripetal location of Kranz chloroplasts in outer bundle sheath cells; E, dense chloroplasts in outer bundle sheath cells and radiate chlorenchyma, note adaxial papillae; F, typical NAD-me type photosynthetic anatomy. A, B, × 100; C, D, × 250; E, F, × 400. A, C, *Smook 5108*; B, *Smook 5120*; D, *Gibbs Russell & Smook 5268*; E, *Smook 5153*; F, *Smook 5110*.

section (Figure 3C–F). Abaxial epidermal cells: central cells of intercostal zones larger and resemble bulliform cells in transection; cuticle thin; no macrohairs, prickles or papillae.

Abaxial epidermis in surface view

Zonation: evident but costal zones overlying 3'vbs often without silica bodies as a result of absence of sclerenchyma strands in association with these bundles. *Intercostal long cells*: elongated (length more than 3 × longer than width), side walls parallel to outwardly bowed, end walls vertical; anticlinal walls very thin and slightly undulating, with degree of sinuosity varying with plane of focus; cell shape varies across individual intercostal zones with two files of bulliform-like cells per intercostal zone; these bulliform-like cells actually represent central files of two intercostal zones but costal zones are poorly differentiated (Figure 4C, D). Very few tall and narrow short cells present. *Stomata*: 2 or 4 files of low dome-shaped stomata per intercostal zone; usually separated by a single elongated interstomatal cell. *Papillae*: absent. *Prickles*: absent. *Microhairs*: bicellular with dehiscent distal cell; only basal cells remain, basal cell elongated with length much greater than width; occur in central files of intercostal zones (Figure 4D). *Macrohairs*: absent. *Silica bodies*: very irregular dumbbell-shaped; horizontally elongated; same width as adjacent long cells. *Costal short cells*: 1 or 3 files of cells comprise costal zones; central file with silica bodies, these alternate irregularly with short to long short cells. Costal zones often not associated with 3'vbs, only present over 1'vbs.

DISCUSSION

In general appearance *P. simulans* closely resembles *P. schinzii*, particularly those forms of both taxa that have rounded or cordate leaf bases. However, the hairy nodes (Figure 1B) and pointed apex of the spikelets (Figure 1D, E) and colour of plant (yellowish green vs. green) of *P. simulans* clearly separate these two taxa (Table 1) (Gibbs Russell *et al.* 1990).

All specimens from Namibia previously assigned to *P. schinzii* have now been re-identified as *P. simulans*. There is one exception, *Volk 2672*. However, there is no habitat information for this specimen, and it may have been a weed from a cultivated land and imported with the crop.

Panicum schinzii and *P. simulans* both tend to be hydrophytic, but they are clearly separated geographically. Their natural populations were undoubtedly originally allopatric, but it can be expected that, with increasing agriculture under irrigation, *P. schinzii* will become established in the range of *P. simulans*.

In addition to the morphological differences between *Panicum simulans* and *P. schinzii*, there are major differences in the photosynthetic leaf anatomy between these two taxa. *P. simulans* has the NAD-me subtype of the C_4 photosynthetic pathway, as the anatomy is Kranz with a double bundle sheath with the specialized chloroplasts of the parenchyma sheath centripetally arranged (Ellis 1988). The *Panicum* species with this type of photosynthetic anatomy constitute the 'true' *Panicum* species (Brown 1977) as *P. miliaceum* L., the type of the genus, belongs to this group.

Panicum schinzii, on the other hand, characteristically has the Kranz chloroplasts located against the outer tangential cell wall. These chloroplasts are relatively small and often form only a thin peripheral layer in contrast to the large, dense chloroplasts of *P. simulans*. The anatomy of *P. schinzii* is typical of that of the PEP-ck subtype of the C_4 pathway (Ellis 1988). Brown (1977) considered all the *Panicum* species of this PEP-ck subtype, as doubtful members of the genus and as belonging to *Brachiaria*, together with *Urochloa* and *Eriochloa*. This applies particularly to those species with rugose lemmas.

Ellis (1988) grouped *Panicum simulans* and *P. schinzii* in two different subgeneric groups because of these distinct anatomical differences. *P. schinzii* was placed in Group 2d whereas *P. simulans* (as *Panicum* spp., together with *P. novemnerve*) was placed in Group 3b.

Group 2, although the leaf anatomy is typically PEP-ck throughout, actually consists of two distinct and separate groups. Group 2d with *P. schinzii*, together with *P. gilvum* Launert, *P. impeditum* Launert, *P. repens* L. and *P. subalbidum* Kunth, are all hydrophytic and have pale, glossy upper lemmas. These taxa are clearly not closely allied to Groups 2a–2c, all of which appear to belong to the panicoid grasses with rugose lemmas. The *P. schinzii* group of species (except *P. repens*) belongs to section *Dichotomiflora* (Hitchc. & Chase) Honda of subgenus *Panicum* (Zuloaga 1987) and is not closely allied to *P. simulans* despite the superficial morphological resemblance.

The work of Ohusigi *et al.* (1982) urges caution in assigning *P. schinzii* and its allies to the PEP-ck photosynthetic subtype as they may actually all be NAD-me. The biochemical typification of these taxa urgently needs verification before final taxonomic decisions can be made. However, this has no bearing on the separation of *P. simulans* from this group.

In the past *P. novemnerve* has also been confused with *P. simulans*. However, *P. simulans* has only one distinct

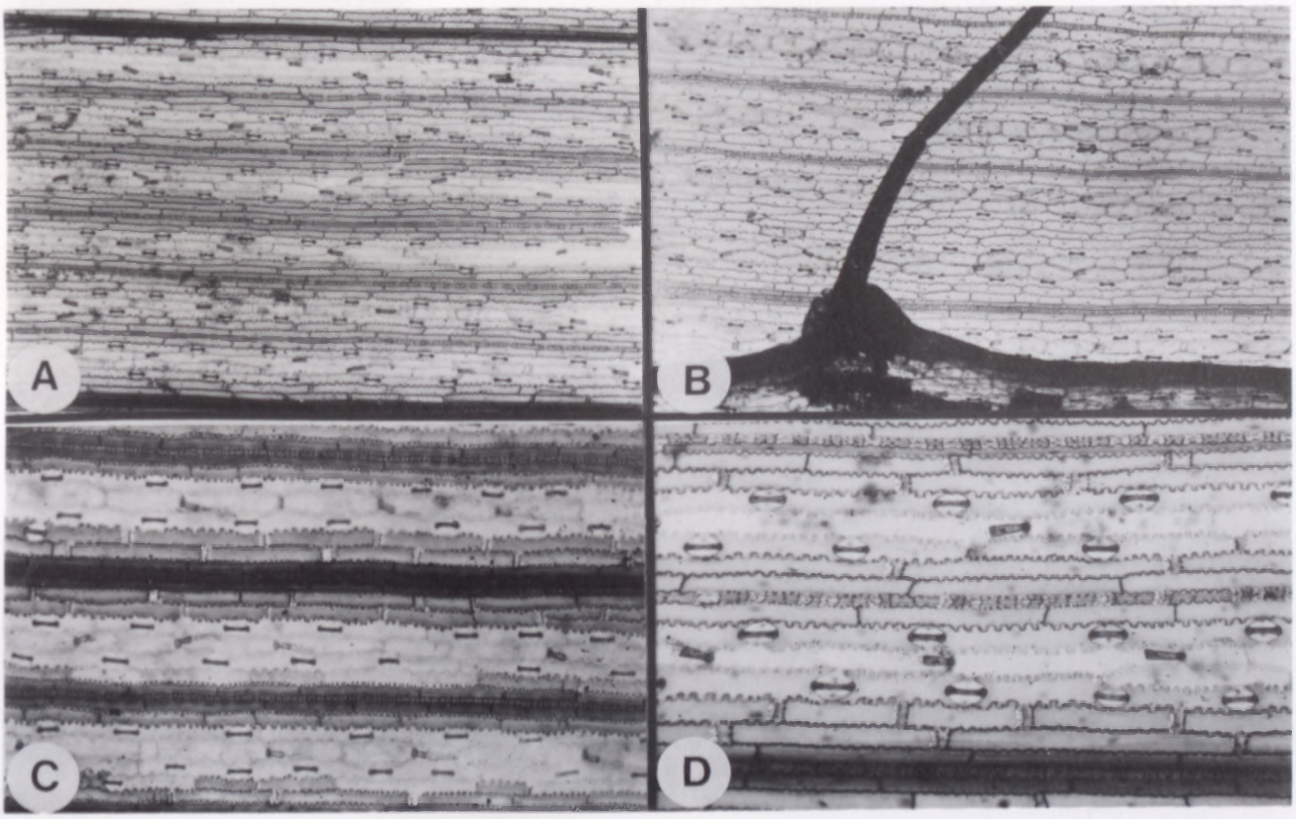

FIGURE 4.—Abaxial epidermal structure of *Panicum simulans*. A, typical zonation pattern with 5 narrow costal zones located over third-order bundles between successive first-order bundles; B, leaf margin showing cushion-based macrohair; C, stomata and microhairs in intercostal zones; D, low dome-shaped stomatal subsidiary cells, basal cells of microhairs and very irregularly dumbbell-shaped silica bodies. A, B, × 160; C, × 250; D, × 400. A, D, *Smook 5153*; B, *Smook 5110*; C, *Smook 5109*.

and obvious nerve on the lower glume (Figure 1D) instead of 3–5 as in *P. novemnerve*. In *P. novemnerve* the lower floret is sterile with a reduced palea (Stapf 1920), whereas in *P. simulans* the lower floret is male with a well-developed palea (Gibbs Russell *et al.* 1990). These two taxa can, therefore, be readily separated on morphological criteria.

Panicum simulans and *P. novemnerve* also share similar damp habitats although *P. novemnerve* appears to prefer shady areas. They are sympatric in Namibia, but *P. novemnerve* also occurs in Botswana and the Transvaal.

The leaf anatomy of *P. novemnerve* (as based on *Smook 5163* and *Gibbs Russell & Smook 5235*) and *P. simulans* is virtually identical. Both have the NAD-me type anatomy with very little sclerenchyma development. The only discernible difference appears to be that the intercostal long cells in *P. novemnerve* are often separated by tall and narrow short cork cells, which is very seldom the case in *P. simulans*. Both *P. simulans* and *P. novemnerve* specimens were included under *Panicum* spp. of Group 3a by Ellis (1988) because of this similarity in leaf blade anatomy. These two annual species, together with *P. arcurameum* Stapf and *P. atrosanguineum* A. Rich., undoubtedly belong to the *P. coloratum* L. group of species, and show very close similarities with *P. pilgerianum* (Schweick.) Clayton [= *Psilochloa pilgeriana* (Schweick.) Launert], another annual hydrophyte. This latter species has only recently been placed in *Panicum*, and this small group of annual species appears to form a clear subgrouping within the *P. coloratum* group of species. They resemble an unnamed perennial entity within *P. coloratum* particularly closely, as discussed by Ellis (1988). Specimens of this taxon are *Ellis 1783, 2905* and *2912*, all of which are also hydrophytes. *Oryzidium barnardii* C.E. Hubb. & Schweick., may also belong to this assemblage.

Panicum simulans, therefore, appears to belong with the 'true' *Panicum* species of section *Panicum* of subgenus *Panicum* (Zuloaga 1987). These are typical NAD-me species as suggested by the leaf anatomy but biochemical typing is required.

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