Euphytica **97:** 1–20, 1997.

Review of *Pennisetum* section *Brevivalvula* (Poaceae)

G.H. Schmelzer
ORSTOM, Genetic Laboratory, B.P. 11416, Niamey, Niger; present address: Department of Plant Taxonomy, P.O. Box 8010, 6700 ED Wageningen, The Netherlands

Received 24 September 1996; accepted 2 April 1997

Key words: apomixis, *Brevivalvula, Pennisetum*, polyploidy, review

Summary

Section *Brevivalvula* is one of five sections in the large tropical grass genus *Pennisetum*. It belongs to the tertiary genepool of *P. glaucum* (L.) R. Br., pearl millet, and consists of six morphological taxa: *P. atrichum* Stapf & Hubb., *P. hordeoides* (Lam.) Steud., *P. pedicellatum* Trin., *P. polystachion* (L.) Schult., *P. setosum* (Swartz) L. Rich. and *P. subangustum* (Schum.) Stapf & Hubb., which together form a polyploid and agamic complex. Four euploid (x = 9) and twelve aneuploid chromosome levels have been found till now; the polyploids are apomictic, while diploid populations of *P. polystachion* and *P. subangustum* are considered sexual.

The genus *Pennisetum* and its sections

The genus *Pennisetum* (bristle grass) is one of the important genera of the tribe *Paniceae*, and is widely distributed throughout the tropics. The best known species is *Pennisetum glaucum* (L.) R. Br., pearl millet, which is the most drought tolerant major cereal cultivated. It is present mainly in subsaharan Africa and India, and can still produce with as little as 250 mm of annual rainfall. *P. purpureum* Schum., elephant grass, is an important fodder species throughout the wet tropics. Several other *Pennisetum* species are agronomically important as forage species or as weeds. Research has been focused over the years on improvement of pearl millet cultivars for grain or forage at the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), India and West-Africa, on the heredity of apomixis in crosses between pearl millet and apomictic taxa (Dujardin & Hanna, 1984a, 1984b, 1989a, 1989b) and on the improvement and use of apomictic fodder species (Patil & Singh, 1980; Whyte, 1964).

Pennisetum has been a difficult genus to classify, and taxa have been placed formerly under a variety of genera: *Penicillaria, Holcus, Panicum, Setaria* and *Cenchrus*, before they settled down in *Pennisetum*. The genus is mainly characterized by its inflorescence: a false spike, with spikelets on contracted axes, or spikelets fascicled in false spikes, always surrounded by involucres; the involucres are crowded, with slender, basally free, glabrous to plumose bristles; the spikelets are sessile or pedicellate, falling with the involucres, only persistent in the cultivated species (Watson & Dallwitz, 1992). The spikelets are lanceolate to oblong, acute to obtuse; the glumes are hyaline or membranous, often unequal, the lower one very small and sometimes absent, the upper one variable, very small to as long as the lemma, with 1–9 nerves. The valve is as long as or shorter than the spikelet, lanceolate to elliptic-oblong, acute, obtuse or truncate, frequently mucronate, rarely 3-lobed. The valvule is narrow, 2-keeled, shorter or as long as the valve, or suppressed; lodicules minute or absent. The seed is mostly oblong and dorsally compressed, obovoid or subglobose (Stapf & Hubbard, 1934).

Estimations of the number of species in the genus vary from 130 to 80 species worldwide (Nath et al., 1971; Purseglove, 1972). In tropical Africa 91 (Stapf & Hubbard, 1934) to 39 (Lebrun & Stork, 1995) species occur, but the actual number can only be determined after a revision of the genus.

Chase (1921), and later Brunken (1977) made systematic studies of pearl millet, in order to clarify the confusion around its name. Nowadays, mostly Chase

(1921) is followed, who determined that *Pennisetum glaucum* (L.) R. Br. is the rightful name for pearl millet. The names *P. typhoides* (Burm.) Stapf & Hubb. and *P. americanum* (L.) Leeke are still used sometimes in publications, but are synonyms. *P. glaucum* belongs to a polymorph species in which three subspecies have been first recognized by Brunken (1977), adapted later by Van der Zon (1992): *P. glaucum* ssp. *glaucum*, the cultivated pearl millet, *P. glaucum* ssp. *violaceum* (Lam.) A. Rich., its putative wild ancestor, and *P. glaucum* ssp. *sieberianum* (Schlecht.) Stapf & Hubb., comprising all the hybrids formed between the first two subspecies. The first two subspecies remain distinct due to pre-zygotic barriers, resulting in an advantage of self-pollination (Sarr et al., 1988; Robert et al., 1991) and post-zygotic barriers, resulting in the reduction in viability of hybrid grains (Amoukou & Marchais, 1993), geographical isolation and partly overlapping flowering periods resulting in an endogamic reproduction of the wild subspecies after the cultivated subspecies finished flowering (Renno & Winkel, 1996). The classification in three subspecies is biologically not valid, although taxonomically convenient.

Harlan (1975) divided the *Pennisetum* species into gene pools on the basis of their genetic and taxonomic relationships with the cultivated species, *P. glaucum* (comprising the three subspecies), which is placed in the primary gene pool, with 2n = 2x = 14. The secondary gene pool includes all biological species that will cross with the primary gene pool, even when the hybrids tend to be sterile. It comprises one more species, *P. purpureum*, with 2n = 4x = 28. The tertiary gene pool is composed of species with basic numbers x = 5, 7, 8, and 9. Of these species the hybrids with the primary gene pool tend to be anomalous, sterile or lethal, and gene transfer is difficult to establish.

As for the sections, most authors accept those recognized by Stapf & Hubbard (1934): *Gymnothrix*, *Pennisetum*, *Penicillaria*, *Heterostachya* and *Brevivalvula*. Only Brunken (1977) included two species of section *Penicillaria* in a different section *Pennisetum*. The differences between the sections are often not very strong and can be summarized as follows: in *Gymnothrix* the spikelets are usually solitary, rarely in clusters of 2–3; the involucres are (sub-) sessile; the bristles are scaberulous, or rarely ciliate; the anthers have glabrous tips, except *P. thunbergii* Kunth. Section *Pennisetum* has 1–4 spikelets in each involucre; the spikelets are, if clustered, all alike in shape and usually in sex, or the outer sometimes male, not keeled; the bristles are ciliate, at least the inner ones. Section *Penicillaria* is further differentiated from other *Pennisetum* species by its penicillate anthers, while section *Heterostachya* has clustered, heteromorphous spikelets, the external male laterally compressed and keeled, the central hermaphrodite. The last section *Brevivalvula* is well differentiated from the other sections by the heteromorphous valves, the lower thinly membranous, often three-lobed, the upper shorter, chartaceous, smooth and shining, truncate or very obtuse, ciliolate at the apex; the rachis has decurrent wings below the scars of the fallen involucres (Stapf & Hubbard, 1934).

In Africa section *Gymnothrix* comprises 22 species when those that were formerly classified under *Beckeropsis* are included (Stapf & Hubbard, 1934). The best known species are the very variable *P. macrourum* Trin., *P. ramosum* (Hochst.) Schweinf., and *P. hohenackeri* Steud. The section *Pennisetum* comprises five species, of which *P. villosum* (R. Br.) Fresen. (feathertop), *P. setaceum* (Forssk.) Chiov. (fountain grass) and *P. clandestinum* Chiov. (kikuyu grass) are most common. Section *Penicillaria* comprises seven species, but five of them are probably better classified as cultivars of *P. glaucum* (L.) R. Br. subsp. *glaucum* (pearl millet); the other species is the well-known fodder grass *P. purpureum* Schum. (napier grass, elephant grass). The section *Heterostachya* comprises two species: *P. squamulatum* Fresen. and *P. tetrastachyum* K. Schum. (syn. *P. schweinfurthii* Pilg.) and according to Lebrun & Stork (1995) section *Brevivalvula* comprises three species, *P. pedicellatum* Trin., *P. polystachion* (L.) Schult. and *P. hordeoides* (Lam.) Steud, two of which are divided into two subspecies each: *P. pedicellatum* subsp. *pedicellatum*, *P. pedicellatum* subsp. *unispiculum* Brunken, *P. polystachion* subsp. *polystachion* and *P. polystachion* subsp. *atrichum* (Stapf & Hubb.) Brunken.

The genus *Cenchrus* is closely related to *Pennisetum*, the main difference being the flattened involucral bristles, which are fused at the base in *Cenchrus*, often forming a cup, whereas in *Pennisetum* they are filiform and not fused. This difference is sometimes marginal: *C. ciliaris* L. (syn. *P. ciliare* Link.) has been shifted between the two genera for a long time, and is obviously morphologically an intermediate form. In this species the disc is only 0.5–1.5 mm large, and only the longest bristle is flattened towards the base (Launert & Pope, 1989). Characteristics which make the species seem more closely allied to *Pennisetum* are the antrorsely scabrous bristles, retrorse in the other *Cenchrus* species, the basic chromosome number of

x = 9 and the extensive occurrence of apomixis (Pohl, 1980).

Species relationships

Several analyses have been conducted the last ten years in order to determine the degree of relationship among the different *Pennisetum* species. They can be divided into analyses that explain species relationships on the basis of qualitative and quantitative phytochemical characters in different taxa, and analyses that explain patterns on a genetical base.

Subba Rao et al. (1988), Husein et al. (1990) and Saideswara Rao et al. (1991) analysed in total 24 different phytochemicals of an almost identical group of 12 *Pennisetum* species. The first authors performed a cluster analysis with the information obtained on 3 aspects, showing neither a strict clustering for species with a same basic chromosome type, nor for species belonging to the same gene pool, nor for a same section. *P. polystachion*, the only species of section *Brevivalvula* analysed, was found to be 60% dissimilar with the other clusters, basically because no protein profile was obtained, and they thus confirmed its belonging to a separate section. The analysis of four isozymes showed that the species relationships among the *Pennisetum* species, originating from all five sections, was often consistent with the available cytogenetic information. In general there was a closer affinity among species of the x = 9 basic number type and among those of the x = 7 type (primary and secondary gene pool). *P. mezianum* Leeke, the only species with a x = 8 type, showed closer relationships with the x = 9 types than with both x = 7 types. There was no particular affinity among the x = 9 species of a same section. Most of the species studied, including *P. polystachion*, showed distinct individual banding patterns. The analysis of 17 free amino acid quantities in leaf extracts revealed no clear information on their phylogenetic affinity, although the profiles in itself were highly species specific. *P. polystachion* showed the least similarity with *P. orientale* (52.9%) and the highest with *P. squamulatum* (100%). No correlation was found with ploidy level.

The results of these phytochemical analyses show basically that the present sections of *Pennisetum* are not based on other than, rather weak, morphological similarities. The clustering of *P. polystachion* into a separate group in the first analysis is based primarily on the absence of certain leaf proteins. This is questionable because no other species of section *Brevivalvula* have been analysed, so no generalisations can be made of the section as a whole. In general, most phytochemicals seem to be rather species specific, which make them useful as biochemical markers.

When the second group of analyses, those with a genetical base, are compared, similar conclusions are reached in part. Lagudah & Hanna (1989, 1990) studied enzyme polymorphism of leaves, and later seed proteins and prolamines, in *Pennisetum*. They used 15 wild species and 21 pearl millet inbreds and landraces, the accessions originating from different tropical regions. The first analysis shows highly polymorphic zymograms in 4 of the 6 isozymes used. They conclude that the choice of a specific enzyme system may lead to variable deductions on phylogenetic relationships in all three gene pools. For example, the three species of section *Brevivalvula* used, *P. polystachion, P. pedicellatum* and *P. subangustum*, are shown to be closely related on the basis of two enzymes, but highly divergent on the basis of another. In the second analysis prolamin polymorphism was found to be much higher in wild than in cultivated pearl millet, while the prolamins found in *P. purpureum*, of the secondary gene pool, show a high similarity with this first group. Differences in prolamin composition were revealed among all species of the tertiary gene pool, caused either by the different geographical origin or sometimes to ploidy level. Compared to sections *Gymnothrix, Eu-Pennisetum* and *Heterostachya*, the 3 species of section *Brevivalvula* showed the highest degree of species relatedness, while within this section *P. subangustum* showed more affinity to *P. polystachion* than to *P. pedicellatum*. Similar results have been obtained by Chowdhury & Smith (1988) based on mitochondrial DNA variation. In this study *P. polystachion* and *P. pedicellatum* shared 89% of the total number of restriction fragments. It was suggested that these two species be considered as one species rather than two, which is questionable because not all species of the section have been analyzed. A more general conclusion of these analyses is that although it is difficult to determine the phylogenetic relationships in especially the tertiary gene pool, section *Brevivalvula* seems to be the only one that is fairly coherent.

Pennisetum section *Brevivalvula*

Although the section *Brevivalvula* is well differentiated from the other sections of *Pennisetum*, the number of taxa in the section is not well defined. Recent flora's (Clayton & Renvoize, 1982; Launert & Pope,

1989; Van der Zon, 1992) follow Brunken (1979b) to some extent. He distinguishes, based on a morphometric analysis of 177 single-plant collections from tropical Africa, three species of which two are subdivided into subspecies, with a total of six taxa. These taxa are: *P. pedicellatum* Trin. subsp. *pedicellatum*, *P. pedicellatum* Trin. subsp. *unispiculum* Brunken, *P. hordeoides* (Lam.) Steud., *P. polystachion* (L.) Schult. subsp. *polystachion*, *P. polystachion* (L.) Schult. subsp. *setosum* (Swartz) Brunken and *P. polystachion* (L.) Schult. subsp. *atrichum* (Stapf & Hubb.) Brunken. Other authors recognize some or all subspecies of *P. polystachion* as individual species (Stapf & Hubbard, 1934; Bor, 1960; Stanfield, 1970) and especially in West Africa *P. subangustum* (Schum.) Stapf & Hubb. is recognized as a separate species from *P. polystachion* subsp. *polystachion* (Stapf & Hubbard, 1934; Koechlin, 1962; Stanfield, 1970; Clayton, 1972; Rose Innes, 1977). Brunken (1979b) did not find clear morphological reasons to even recognize *P. subangustum* as a subspecies of *P. polystachion* though.

Key to the species

During several fieldtrips in West-Africa (Renno et al., 1995) six taxa, covering the largest polymorphism of the section and considered as morphological species, have been recognized. These species are: *P. pedicellatum* Trin., *P. hordeoides* (Lam.), Steud, *P. polystachion* (L.) Schult, *P. subangustum* (Schum.) Stapf & Hubb., *P. atrichum* Stapf & Hubb. and *P. setosum* (Swartz) L. Rich. They are differentiated as follows, based on Stapf & Hubbard (1934):

1. Spikelets in clusters of 1–5 within the involucre, at least one of the spikelets upon a pedicel of 1–3 mm long; bristles densely woolly plumose, forming a fluffy ovate involucre of 0.5–1 cm long; spikelets 4–6 mm long; colour of involucres white, pink, red or purple ..... *P. pedicellatum*
   Spikelets solitary and sessile within the involucre 2
2. Bristles, or at least the inner ones, plumose to ciliate in the lower half 3
   Bristles glabrous, or the longer ones obscurely ciliate 5
3. Plants perennial, sparingly branched: Spikelets 3–5 mm long; false spike 8–10 mm broad, excluding the bristles; longest bristle 10–25 mm long, the other bristles more than twice as long as the spikelet; colour of involucres yellow, light brown or purplish ..... *P. setosum*
   Plants annual, profusely branching from the lower part; colour of involucres white, pink, red or deep purple 4
4. Spikelets 3–5 mm long; false spike 8–10 mm broad, excluding the bristles; longest bristle 15–25 mm long, the other bristles mostly more than twice as long as the spikelet ..... *P. polystachion*
   Spikelets 2.5–3 mm long; false spike 3–7 mm broad, excluding the bristles; longest bristle 6–12 mm long, the bristles less than twice as long as the spikele ..... *P. subangustum*
5. Plants annual: False spike 4–6 mm broad, excluding the bristles; longest bristle 5–8 mm long, the others in 1 whorl of 6–11 and subequal to the spikelet to 1.5 times as long; spikelets 2.5–3.5 mm long; colour of involucre and spikelet red and/or white ..... *P. hordeoides*
   Plants perennial: False spike 7 mm broad, excluding the bristles; largest bristle 11–16 mm long, the others irregularly 2-whorled and up to twice as long as the spikelet; spikelets 3–4 mm long; colour of involucre and spikelet yellow ..... *P. atrichum*

Geographical distribution

Pennisetum section *Brevivalvula* is widely spread in tropical Africa, with West Africa as the probable centre of diversity, because all species are present here (Stapf & Hubbard, 1934). All species except *P. atrichum* migrated (or were introduced) to India, and *P. pedicellatum*, *P. polystachion* and *P. setosum* migrated probably from there to South East Asia and Northern Australia. One species, *P. setosum*, has found its way even to the new world (Hitchcock, 1936, 1950; Luces de Fèbres, 1963). A more comprehensive recapitulation of the individual species is given below:

P. hordeoides has always been classified as a separate species. Its distribution area is West Africa (Rattray, 1960), and southwards to Zaire, Gabon and Angola (Figure 1a). It is not mentioned to occur in East Africa (Stapf & Hubbard, 1934). The species is also present in India, in the northern humid regions (Stapf & Hubbard, 1934; Bor, 1960).

It is a slender annual species, often much branched, with small involucres. The bristles are few and bare so that the spikelet, often reddish tinged, is visible. It is a weed of cultivation, and covers often considerate areas under subhumid conditions. It is also locally abundant on disturbed sandy or gravelly sites, chiefly roadsides.

P. pedicellatum is widely distributed in West Africa (Rattray, 1960; White, 1986), except for the rain

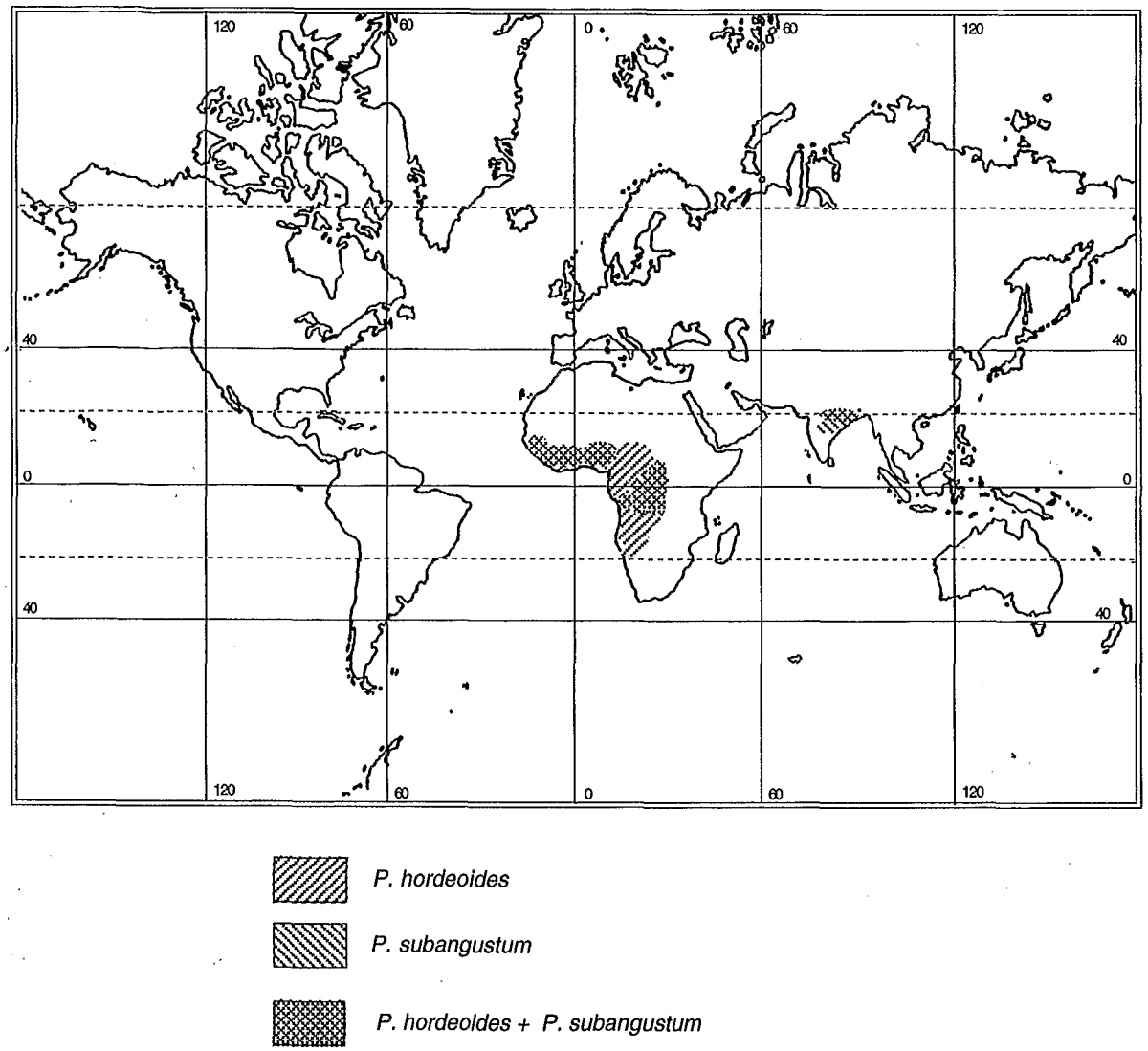

Figure 1A. Geographical distribution of *P. hordeoides* and *P. subangustum*

forest area in the south, but including the Cap Verdiane islands. The area is extended eastwards towards Ethiopia (Stapf & Hubbard, 1934), and Tanzania (Clayton & Renvoize, 1982). The species is also mentioned in Zambia (Clayton & Renvoize, 1982; Kativu & Mithen, 1988), but not in Zaire or other countries in southern Africa (Figure 1b). It also occurs in India (Stapf & Hubbard, 1934; Bor, 1960) and has been introduced in South East Asia and western and northern Australia (Hafliger & Scholz, 1980; Webster, 1987; Lonsdale & Lane, 1994).

It is a profusely branching annual, rarely perennial, species, up to 1.2 m high, with big, fluffy inflorescences. It is often dominant upon fallow land in the drier savanna, on sandy soils, and is also found around villages, on the banks of rivers, or as a weedy species on disturbed sites and road verges. It is one of the first to appear at the beginning of the rainy period.

P. pedicellatum is known as a weed in grain sorghum crops in northern Australia, and is effectively controlled by hygiene, combined with minimum tillage and herbicide application. In pasture, heavy grazing prevents seed set (Groves, 1991). Maillet (1991) lists it

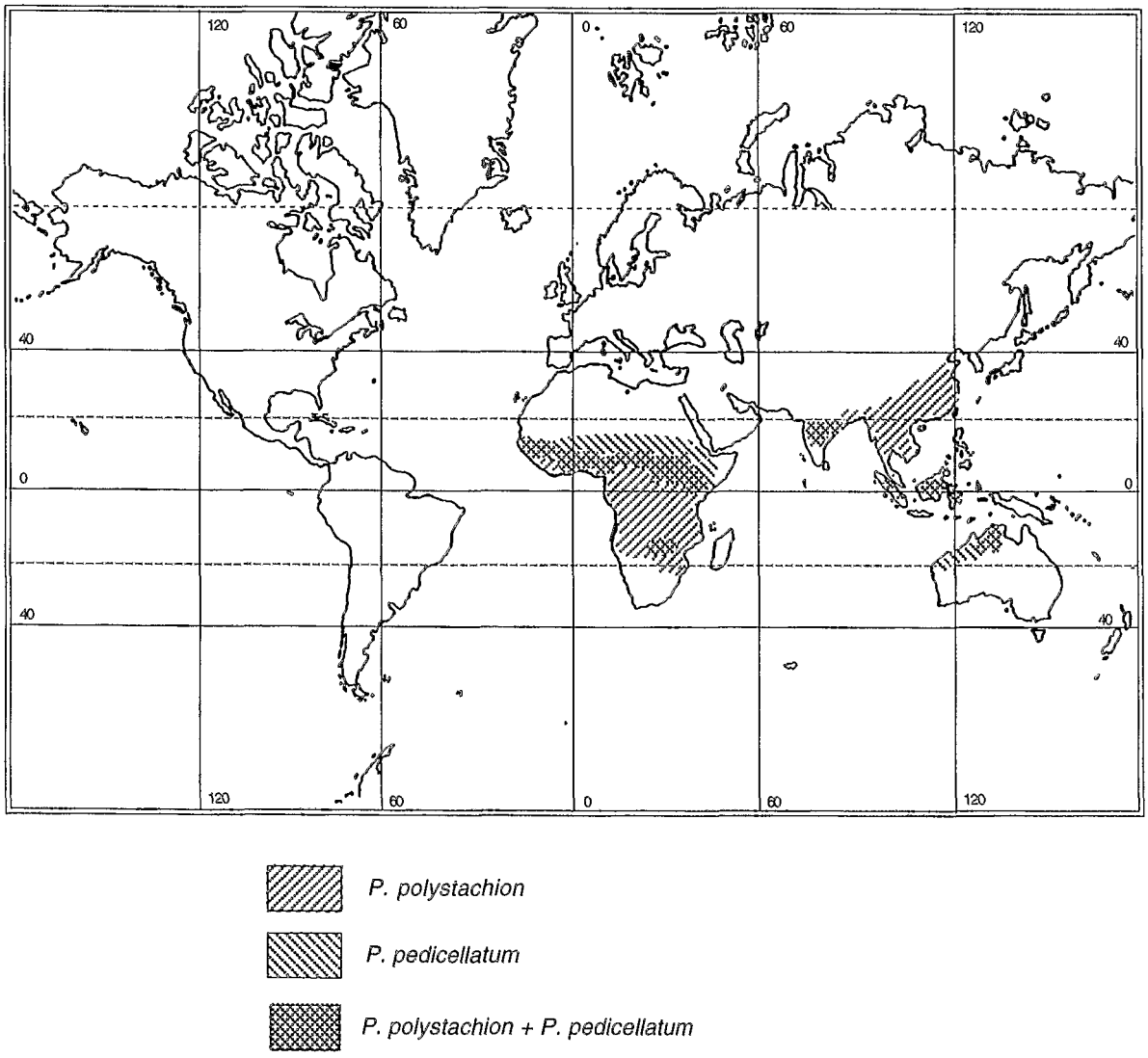

Figure 1B. Geographical distribution of *P. polystachion* and *P. pedicellatum*

among the most important, locally abundant weeds, in tropical cereals, especially in well-fertilized sorghum and pearl millet fields in Africa and Asia. Terry (1991) lists it erroneously among the perennial grasses of secondary importance in the world, while it is normally an annual. In the north of Cameroun, it is an important weed in late weeded fields, because the robust bunches are difficult either to turn over to dry out or to bury. Contact herbicides have only a limited success, because the plant can form new tillers from hidden nodes (Le Bourgeois & Merlier, 1995).

P. polystachion is distributed in tropical Africa, including the Cap Verde Islands (White, 1986) over a larger area than *P. atrichum*, for it grows also under drier conditions (Figure 1b). Its presence in South East Asia is uncertain despite the fact that its presence is often mentioned here, but mostly the perennial species, *P. setosum*, is meant (Hafliger & Scholtz, 1980; Skerman & Riveros, 1990; Tjitrosoedirdjo, 1990). Webster (1987) mentions the presence of *P. polystachion* subsp. *polystachion* in Australia, but adds in the description that the plants are annual or perennial, while the subsp. *polystachion* is an annual (Brunken, 1979b).

It is a profusely branching annual species, up to 1.5 m high, more robust than *P. subangustum*. It grows on old farmland and waste places, and is very common,

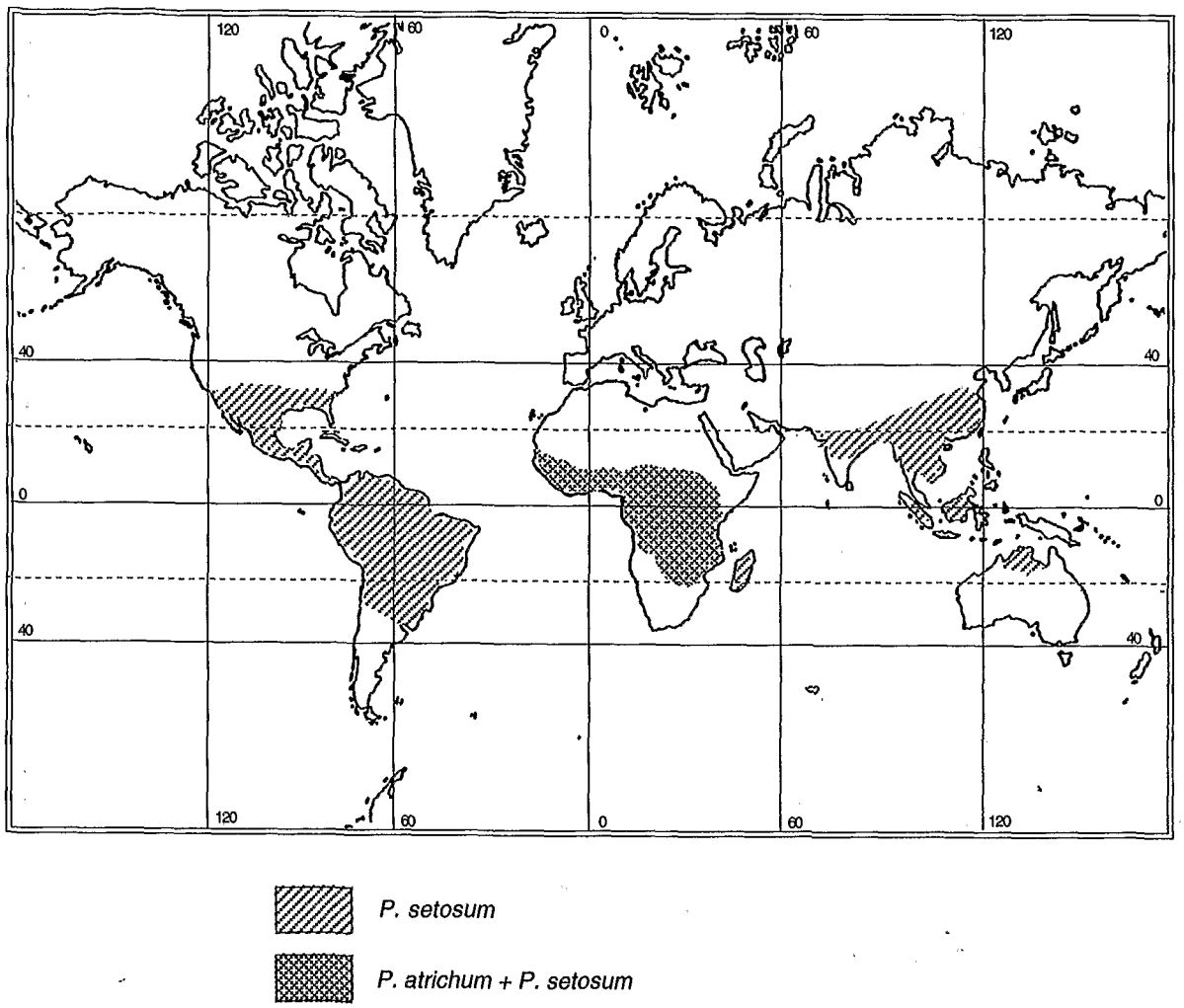

Figure 1C. Geographical distribution of *P. setosum* and *P. atrichum*

especially as a secondary weed of disturbed roadsides, fallow land and villages. It provides good grazing during the rainy season (Rose Innes, 1977). Maillet (1991) lists it among the most important weeds in sorghum and pearl millet in Africa and Asia. Le Bourgeois & Merlier (1995) mention its presence in crops the same way as *P. pedicellatum*. Lonsdale & Lane (1994) found the involucres of *P. polystachion* being dispersed on the wheels of tourist vehicles in a national park in northern Australia, and valuated it as one of the most dangerous introduced grass weeds there. No mention was made of its lifecycle.

The name *P. polystachion* seems to be particularly prone to misspelling. The orthographic variant *P. polystachyon* is very commonly encountered, and even *P. polystachyum* occurs.

P. atrichum has a continuous distribution from Senegal in West Africa towards Kenya in East Africa and towards Zimbabwe in southern Africa (Figure 1c). It is mentioned either as a distinct species (Stapf & Hubbard, 1934; Jackson & Wiehe, 1958; Napper, 1965; Stanfield, 1970; Clayton, 1972) or more recently, as a subspecies of *P. polystachion* (Brunken, 1979b; Clayton & Renvoize, 1982; Launert & Pope, 1989; Van der Zon, 1992), which comprises annual and perennial taxa.

It is a perennial species, growing in leafy clumps till 1.8 m high, with few branches. It grows under relative-

ly humid conditions in tree savanas, or in seasonally flooded or damp grassland, on sandy or clay soils.

P. setosum is mentioned either as a distinct species (Hitchcock, 1936, 1950; Bor, 1960; Luces de Febres, 1963), as a synonym of *P. polystachion* (Stapf & Hubbard, 1934; Koechlin, 1962; Clayton, 1972; Launert & Pope, 1989), but then with the remark that the annual and perennial types are mixed, or as *P. polystachion* subsp. *setosum* (Brunken, 1979b; Van der Zon, 1992). It has the largest distribution area of section *Brevivalvula* (Figure 1c). It occurs in the whole of tropical Africa, in the subhumid to humid regions. The taxon has been introduced in India, the whole of south East Asia, the Pacific islands, and northern Australia, as well as tropical America, and there it occurs from Brazil to the south of Florida in the United States.

It is a short or long living perennial, up to 2 m high, flowering in its first year, and then resembling an annual, especially on poor soils. The species grows in clumps, with many basal leaves, and relatively few branches. It is widespread in the more humid regions, common in early stages of recolonisation of abandoned cultivation and road sides. It is a noxious spreading weed in rubber plantations (Tjitrosoedirdjo, 1990), as well as oil palm plantations, orchards, vegetable and upland rice farms. Regrowth can occur from dormant buds located at the basal stem area and from the aerial nodes of the stem. As a fire disclimax, *P. setosum* invades a good deal of the mountainous land in Fiji and Thailand, and it is generally seen as a weed (Skerman & Riveros, 1990). Control by slashing does not control the plants completely, because of its easy regrowth; contact herbicides are used in plantation crops, but repeated application is necessary (Tjitrosoedirdjo, 1990).

Of *P. subangustum* it is difficult to assess its distribution area because it is often integrated in the polymorphic species *P. polystachion*, as a synonym (Brunken, 1979b; Clayton & Renvoize, 1982; Van der Zon, 1992). Before Brunken (1979b) it was classified as a separate species (Stapf & Hubbard, 1934; Chase & Niles, 1962; Koechlin, 1962; Stanfield, 1970; Clayton, 1972; Rose Innes, 1977). Herbarium material contains mostly specimens from West Africa (pers. obs. Kew, Paris, Wageningen), with few specimens originating from central Africa (Zaire, Gabon), in a discontinuous pattern (Figure 1a). It is a common species in the savanna of the southern half of Senegal (Stancioff et al., 1986). It has been introduced to India in the fifties, possibly with seed samples originating from Nigeria (Chatterjee & Kumar, 1964).

It is an annual species, up to 1.2 m high, with notably narrow inflorescences. It grows on fallow land and disturbed soils, with numerous other secondary weeds, under subhumid conditions. It is one of the dominant species in fallowed rice fields in Sierra Leone (Nyoka, 1982), in association with *P. hordeoides* (Rattray, 1960).

P. polystachion and *P. setosum* are often considered to be only one species, *P. polystachion*, which has an annual or perennial lifecycle. It is true that these species can not easily be separated in herbarium material, because often only the upper parts of the flowering culms have been collected, so that neither the branching pattern, nor the basal leaves, nor the root system can be evaluated, but this is mainly a collection problem. Another difficulty for proper identification is that the often yellowish to reddish colour of the inflorescences of *P. setosum* does not keep well in a dried state. The controversy of the lifecycles of both species has probably arisen because of their introduction into regions with different growth seasons. *P. setosum*, the perennial species, does not support long periods of drought, and will die some months after the rains have stopped. It thus behaves as an annual, but will become perennial in regions with a continuous rainy season, or a short dry season. It is not a strong species, prone to overgrazing (Skerman & Riveros, 1990) and in that case possibly does not survive many years. If allowed to grow and flower undisturbed though, it becomes perennial. *P. polystachion*, on the contrary, will die once it has flowered, even with a continuous rainy season.

Cytology of section *Brevivalvula*

The genus *Pennisetum* is cytologically very heterogeneous, chromosome numbers in the species range from 2n = 10 to 2n = 78, with basic numbers x = 5, 7, 8 and 9, while aneuploids are fairly common.

Brunken (1979a) and Jauhar (1981) cite a fairly complete list of chromosome numbers found in the taxa of *Pennisetum* section *Brevivalvula* (x = 9). A revised version of the chromosome numbers found in this section is given in Table 1. A total of four euploid and twelve aneuploid levels is found, respectively 2n = 18, 36, 45 and 54, and 2n = 24, 30, 32, 35, 35 + 1B, 42, 48, 52, 53, 56, 63 and 78. The only species with all four euploidy levels is *P. polystachion*, 2n = 18, 36, 45 and 54, and three aneuploid numbers (2n = 48, 52 and 63). *P. pedicellatum* follows with three euploid levels, 2n = 36, 45, and 54, but most aneuploids have been

Table 1. Chromosome numbers of *Pennisetum* section *Brevivalvula*

Species	2n	References
P. atrichum	36	Brunken (1979a)
P. hordeoides	18	Khosla & Mehra (1973)
	36	Renno et al. (1995)
	54	Renno et al. (1995)
P. pedicellatum	24*	Joshi et al. (1959)
	30*	Chatterji & Pillai (1970)
	32*, 35*	Carnahan & Hill (1961)
	35 + 1B*	Brunken (1979a)
	36	Brunken (1979a), Nath et al. (1971), Nath & Swaminathan (1957), Olorode (1974), Patil et al. (1964), Rangasamy (1972), Veyret (1957), Yadav et al. (1980), Renno et al. (1995)
	42*	Chatterji & Sahu (1982)
	45	Brunken (1979a), Renno et al. (1995)
	48*	Joshi et al. (1959), Chatterji & Das (1979), Chatterji & Sahu (1982)
	52*	Brunken (1979a)
	53*	Yadav et al. (1980)
	54	Brunken (1979a), Khosla & Mehra (1973), Mitra & Datta (1967), Nath et al. (1971), Nath & Swaminathan (1957), Olorode (1975), Sisodia (1970), Rangasamy (1972), Yadav et al. (1980), Renno et al. (1995)
P. polystachion	18	Renno et al. (1995)
	36	Brunken (1979a), Pantulu (1969), Renno et al. (1995)
	45	Brunken (1979a), Renno et al. (1995)
	48*	Gould & Soderström (1974)
	52*	Gould & Soderström (1974)
	54	Brunken (1979a), Gould & Soderström (1974), Krishnaswamy & Raman (1949), Mitra & Datta (1967), Olorode (1975), Singh & Godward (1960), Sisodia (1970), Rangasamy (1972), Renno et al. (1995), Tateoka (1965)
	63*	Muniyama & Narayan (1975)
P. setosum	53*	Pohl & Davidse (1971)
	54	Brunken (1979a), Hrishi (1952), Renno et al. (1995)
	56*	Brunken (1979a)
	78*	Gould (1965)
P. subangustum	18	Renno et al. (1995)
	24*	Joshi et al. (1959)
	32*	Joshi et al. (1959)
	36	Krishnaswamy et al. (1954), Rangasamy (1972), Renno et al. (1995), Veyret (1957)
	54	Olorode (1975), Renno et al. (1995)

* Aneuploids.

determined here, 9 in total (2n = 24, 30, 32, 35, 35 + 1B, 42, 48, 52, 53). *P. subangustum* shows two euploid (2n = 36 and 54) and two aneuploid (2n = 24 and 32) levels, while *P. setosum* is a predominant hexaploid species (2n = 54), with three aneuploid chromosome numbers found (2n = 53, 56 and 78). *P. atrichum* (2n = 36) is the only species without a variation in chromosome numbers, but this could be due to the fact that the species is underrepresented in cytological studies. Of *P. hordeoides* three euploid levels have been determined (2n = 18, 36 and 54), but no aneuploids. The diploid sample (2n = 18) of *P. hordeoides* was the only one of this level known to exist for a long time, leading to some hypotheses by Brunken (1979a) about the hybrid origin of some of the taxa in the section. Other diploids, of *P. polystachion* and *P. subangustum*, were found recently though, in the Banfora area in Burkina Faso by Renno et al. (1995), which throws a different light on the possible origins of the section.

The recurrent statement that two basic numbers, x = 8 and 9, are found in a same species (Joshi et al., 1959; Vishnuvardhan & Laksmi, 1989), is based on the assumption that the chromosome number 48 is a hexaploid with x = 8. Chatterji & Das (1979) found three ploidy levels in four biotypes of *P. pedicellatum*, 2n = 36, 48 and 54, and later Chatterji & Sahu (1982) found four different ploidy levels in five biotypes, 2n = 36, 42, 48 and 54. In this last study two biotypes had both 2n = 36 and 54, a third one showed 2n = 36 and 42. The other biotypes have either 2n = 36 or 48. The authors suppose that the ploidy level 2n = 48 is due to a drop of the basic number from x = 9 to x = 8, called erroneously 'polyploid drop', indicating that the species is in an active state of evolution. It is not less plausible though, as 2n = 48 has been found in the two species with the largest variation in ploidy numbers, *P. pedicellatum* and *P. polystachion*, that 2n = 48 is an aneuploid number, originating from the pentaploid 2n = 45, with x = 9 and its number has become fixed through apomixis, thus constituting an agamic aneuploid complex.

Most aneuploid numbers in the section were determined in chromosome counts in pollen mother cells (PMCs), not on the basis of chromosome counts in somatic cells. Renno et al. (1995) did not find any aneuploids in the section, despite the large *Brevivalvula* sample (304) which was passed through DAPI flow cytometry. The polyploid taxa of section *Brevivalvula* are highly apomictic (see next chapter), and pollen viability (mostly determined as pollen stainability) is often reduced due to a high percentage of aberrant meiosis in PMC (Hrishi, 1952; Naithani & Sisodia, 1966; Nath et al., 1970; Sisodia, 1970; Brunken, 1979a; Sharma et al., 1980; Sisodia & Raut, 1980; Birari, 1981a; Vishnuvardhan & Lakshmi, 1989; Dujardin & Hanna, 1984b). Chromosome counts in PMCs will therefore show a large amount of aneuploid cells, but these aneuploid numbers are normally not reflecting somatic chromosome numbers in any progeny, partly because many pollen cells are not viable and partly because pollination in pseudogamic taxa, which is the case in section *Brevivalvula*, is only necessary for endosperm formation, not for the development of the egg cell. The chromosome numerical mosaicism observed in PMCs of some biotypes of *P. pedicellatum* does not indicate polyaneuploid series nor intra-individual aneuploidy somatically, as is suggested by Vishnuvardhan & Laksmi (1989).

The statement of Jauhar (1981) that polyploid series have been found in the following perennial, vegetatively propagated forage species: *P. hordeoides*, *P. pedicellatum*, *P. polystachion* and *P. subangustum*, among species of other sections, is incorrect. They are all annual grasses, propagating solely through seeds, while only *P. pedicellatum* is known as a forage species.

Nature of polyploidy

The *Poaceae* are characterized by the occurrence of polyploid taxa. Of the genus *Pennisetum*, nearly 76% are polyploids (Jauhar, 1981). There are basically two types of polyploids: autopolyploids, which are composed of multiple sets from within one species, and allopolyploids, which are composed of sets from different species. In autopolyploids, for instance an autotetraploid, the four chromosomes have several possibilities to pair and segregate in mitosis and meiosis, because they are homologous. Paired chromosomes, like in diploids, are called bivalents, pairing of three chromosomes are called trivalents, and pairing of four chromosomes are called quadrivalents, while one unpaired chromosome is a univalent. Bivalents and quadrivalents are most common. With higher ploidy levels, other multivalents can occur (Griffiths et al., 1993). True autopolyploids are rare in nature because the formation of trivalents and univalents are the main causes of aneuploidy, causing various levels of sterility; expression of variability is masked by homozygoty, and they lack vigor (Jauhar, 1981). Allopolyploids are formed between related species; because the chromosomes are only partially homologous, pairing of more than two chromosomes is less common. True allopoly-

Table 2. Multivalent configurations in *P. pedicellatum*

2n	Multivalents							References
	I	II	III	IV	V	VI	VIII	
36		18.00						Rangasamy (1972)
		18.00						Sharma et al. (1980)
		13.30		2.50				Chatterji & Das (1979)
	0.20	16.50		0.70				Nath et al. (1970)
	0.75	11.75	0.27	2.74				Brunken (1979a)*
	0.94	11.84	0.31	2.61				Brunken (1979a)
	0.05	16.50	0.05	0.70				Patil et al. (1964)
	0.75	15.25	0.45	0.85				Pantulu (1969)
45	2.80	8.80	1.30	2.30	2.30			Brunken (1979a)
	4.00	11.20	2.20	1.50	1.20			Brunken (1979a)*
48	0.33	12.50		5.70				Chatterji & Das (1979)
54	6.00	19.00		1.00		1.00		Naithani & Sisodia (1966)
	0.79	24.00	0.38	0.90		0.53		Pantulu (1969)
	4.30	19.10	0.90	0.80		0.90		Vishnuvardhan & Lakshsmi (1989)
	5.74	18.58	0.13	1.17		1.00		Sisodia (1970)
	6.56	17.56	0.31	1.50		1.00		Sisodia & Raut (1980)
	1.80	5.60	1.40	1.70		0.50		Vishnuvardhan & Lakhsmi (1989)
	0.18	15.60	0.40	5.10	0.10	0.13		Chatterji & Das (1979)
	2.32	13.32	0.86	3.42	0.46	1.08		Brunken (1979a)
	0.50	11.10	0.40	3.10	0.30	2.70		Brunken (1979a)*
	1.60	19.00	0.80	2.70	0.06	0.20	0.06	Chatterji & Das (1979)

* *P. pedicellatum* ssp. *unispiculum*.

ploids are usually only formed during hybridization tests, in nature the parental species are rarely completely differentiated. Intermediate situations between auto- and allopolyploids – hemi-autopolyploids, auto-allopolyploids, or segmental alloploids – arise when the species are closely related, and the difference between homologous chromosomes is small. In that case multivalent formation is possible, and herewith the exchange of chromosomes of different parentage (Sybenga, 1968). It will depend on the affinity among the chromosomes whether the auto- or the allopolyploid nature will dominate in the end. Another possibility is that the autopolyploid nature of a species is not expressed, by little multivalent formation. Segmental alloploids are probably preponderant in nature.

In *Pennisetum* section *Brevivalvula*, many studies have been undertaken to understand the pairing behaviour of the chromosomes of the species. Mostly PMCs were counted at metaphase I. Multivalent configurations of *P. pedicellatum* are listed in Table 2. The tetraploids show either only bivalent formation (Rangasamy, 1972; Sharma et al., 1980), which indicates an allopolyploid origin, or also multivalent formation, with uni-, tri- and quadrivalents, the latter being the most frequent. On the basis of these multivalent formations, Patil et al. (1964) and Pantulu (1969) conclude to an autopolyploid origin, despite the high bivalent frequencies. For the higher polyploidy levels, mostly Metaphase I cells with multivalents have been observed, and Pantulu (1969) and Brunken (1979a) suppose a probable autoploid origin, while others suggest an auto-alloploid origin (Rangasamy, 1972; Sharma et al., 1980) or a segmental alloploid origin because of the relatively high number of univalents (Naithani & Sisodia, 1966; Sisodia, 1970; Sisodia & Raut, 1980). The multivalent frequency observed by Pantulu (1969) however, is very low for an autopolyploid.

Multivalent configurations of the other *Brevivalvula* species are given in Table 3. Three ploidy levels (2n = 36, 45, 54) in *P. polystachion* have been analyzed, mostly with multivalent formation, except for the three hexaploids with only bivalent formation (Hrishi, 1952; Sisodia, 1970; Rangasamy, 1972). These hexaploids belong probably to *P. setosum*, the perennial hexaploid species. Some authors tend to an autoploid nature of *P. polystachion* (Pantulu, 1969; Brunken, 1979a), while others more carefully incline to an auto-alloploid origin (Birari, 1981a; Dujardin & Hanna, 1984b). Jauhar

Table 3. Multivalent configurations in the other species of section *Brevivalvula*

Species and 2n	Multivalents I	II	III	IV	V	VI	VIII	References
P. polystachion								
36	0.35	14.85	0.05	1.45				Pantulu (1969)
	0.75	11.75	0.27	2.74				Brunken (1979a)
45	4.20	8.40	1.50	2.10	2.10	0.10		Brunken (1979a)
54		27.00						Hrishi (1952)
		27.00						Sisodia (1970)
		27.00						Rangasamy (1972)*
	2.04	23.30	0.08	0.74				Pantulu (1969)
	1.84	13.96	0.92	3.68	0.20	0.96		Brunken (1979a)
	9.31	19.78	0.72	0.38		0.20	0.03	Birari (1981a)
	0.65	15.58	0.30	3.43	0.10	0.90	0.14	Dujardin & Hanna (1984)
P. subangustum								
36		18.00						Rangasamy (1972)**
P. atrichum								
36	1.73	5.46	1.20	3.20	0.67	0.60		Brunken (1979a)
P. setosum								
54	3.20	11.00	1.21	3.26	0.50	1.60		Brunken (1979a)

* 67.4% of the cases, rest showed 1-2 quadrivalents.
** 95% of the cases, rest showed 1-3 quadrivalents.

(1981) evaluates the sample of Pantulu (1969) as segmental allotetraploids. Multivalent formation comprises uni-, tri- and quadrivalents, with mostly quadrivalents, in the tetraploids. Hexavalents are always present in the penta- and hexaploids, and sometimes penta- or octovalents. In a study on *P. subangustum* (2n = 36) mostly bivalents were counted (95%), in the other cases bivalents and univalents (Rangasamy, 1972). He concludes to an autopolyploid nature of the sample, but with a reduced number of quadrivalents, while Jauhar (1981) contests this on the basis of the regular bivalent formation, indicating an allopolyploid nature. The only analysis of *P. atrichum* (2n = 36) shows multivalent formation, ranging from uni- to hexavalents, and the species is considered an autopolyploid, probably with reduced multivalents, by Brunken (1979a). *P. setosum* (2n = 54) shows, if the analyses by Hrishi (1952) Sisodia (1970) and Rangasamy (1972) are taken into account, predominantly bivalent formation, and the authors conclude unanimously to an allohexaploid nature of the species. Only the sample analyzed by Brunken (1979a) is different, with multivalent formation ranging from uni- to hexavalents, with a relatively high amount of uni- and quadrivalents. His conclusion is that the species has possibly an autoploid origin.

Apomixis in *Pennisetum*

Apomixis, in the sense of agamospermy or asexual seed formation, is a phenomenon especially encountered in the families *Asteraceae*, *Rosaceae* and *Poaceae*, which together comprise about 10% of the angiosperm species (Nogler, 1992). In the *Poaceae* apomixis occurs as four nucleate apospory in the tribes *Paniceae* and *Andropogoneae* (Brown & Emery, 1958). In *Pennisetum*, 14 species (as well as *Cenchrus ciliaris* L.) have been found to reproduce through apomixis so far (Table 4). All species are polyploids with x = 9, except *P. massaicum* Stapf with x = 8, most of them with several euploid or aneuploid chromosomal races. Of *Cenchrus ciliaris* (Bashaw, 1962), *P. flaccidum* Griseb. (Mehra & Remanandan, 1973), *P. massaicum* (Jauhar, 1981), and *P. orientale* L.C.M. Rich. (Jauhar, 1981), sexual diploids have been found to exist, apart from apomictic polyploid cytotypes. The analyzed cytotypes of *P. frutescens* Leeke, *P. latifolium* Spreng., *P. macrourum* Trin., *P. setaceum* (Forsk.) Chiov., *P. squamulatum* Fresen. and *P. villosum* R.Br. Ex Fresen., all had an apomictic reproduction, except for a tetraploid sample of *P. flaccidum*, which was found to be sexual (Mehra & Remanandan, 1973), another tetraploid sample being apomictic (Chatterji & Timothy, 1969a). Not all authors have indicated

Table 4. Ploidy level and relation to type of reproduction in *Pennisetum* and *Cenchrus ciliaris*

Species	Ploidy level	Type of reproduction*	References
P. dubium	polyploids	FAC	Gildenhuys & Brix (1959)
P. flaccidum	5x	APO	Mehra & Remanandan (1973)
	4x	APO	Chatterjee & Timothy (1969a)
		SEX	Mehra et al. (1968), Mehra & Remanandan (1973)
	2x	SEX	Mehra & Remanandan (1973)
P. frutescens	7x	APO	Jauhar (1981)
P. latifolium		APO	Narayan (1955)
P. macrourum	6x	OBL	Dujardin & Hanna (1984b)
P. massaicum	4x	FAC	D'Cruz & Reddy (1968)
		OBL	Shantamma & Narayan (1977)
	2x	SEX	Jauhar (1981)
P. orientale	4x	OBL	Chatterjee & Timothy (1969b)
	4x	APO	Rangasamy (1972)
	polyploids	FAC	Narayan (1951), Simpson & Bashaw (1969), Jauhar (1981)
	2x	SEX	Jauhar (1981)
P. setaceum	3x	APO	Avdulov (1931), Jauhar (1981)
		OBL	Rangasamy (1972)
		FAC	Hrishi (1952)
	6x	APO	Simpson & Bashaw (1969)
P. squamulatum	6x	OBL	Dujardin & Hanna (1984b)
P. villosum	5x	APO	Narayan (1955), Jauhar (1981)
		OBL	Rangasamy (1972)
Brevivalvula			
P. polystachion	6x	FAC	Birari (1981b)
		OBL	Dujardin & Hanna (1984b), Chowdhury & Smith (1988)
	4x	APO	Jauhar (1981), Renno et al. (1995)
P. pedicellatum	polyploids	FAC	Chatterji & Pillai (1970)
	polyploids	OBL	Kallyane & Chatterji (1981)
	4x	APO	Renno et al. (1995)
	6x	APO	Nath et al. (1971), Jauhar (1981)
P. subangustum	4x	APO	Lubbers et al. (1994)
	2x	SEX	Renno et al. (1995)
P. hordeoides	4x	APO	Renno et al. (1995)
P. setosum	polyploids	APO	Jauhar (1981)
Cenchrus ciliaris	polyploids	APO	Fisher et al. (1954), Snyder et al. (1994)
	4x	OBL	Read & Bashaw (1969), Taliaferro & Bashaw (1966)
	2x	SEX	Bashaw (1962)

* APO = apomixis.
FAC = facultative apomixis.
OBL = obligate appomixis.
SEX = sexual reproduction.

the type of apomixis found, in which case the type of reproduction is indicated with APO (apomixis), otherwise with FAC (facultative apomixis) or OBL (obligate apomixis).

In the section *Brevivalvula*, apomixis has been found in *P. pedicellatum, P. polystachion, P. setosum, P. subangustum* and *P. hordeoides*, but the studies in the last three species have been preliminary and require to be studied in detail at this moment. *P. subangustum* (Renno et al., 1995) is the only species in the section where sexual diploids have been discovered. These results are consistent with Asker & Jerling (1992) who

state that agamic polyploid complexes are generally polyploid, and the related sexuals diploid. Section *Brevivalvula* is a special case, because apomixis is found in annual and perennial species, while agamic complexes are normally only found in perennials. Schmelzer & Renno (in press) have not observed a significant variation of the genetic diversity in relation to the ploidy level (diploid sexuals and polyploid apomicts) in the taxa of section *Brevivalvula* studied.

Narayan (1955) has found apomixis in *P. ramosum* (Hochst.) Schweinf., *P. clandestinum* Hochst. ex Chiov. and *P. hohenackeri* Hochst. ex Steud., and Brown & Emery (1958) in *P. purpureum* Schumach., but these tendencies have not been confirmed in material from other sources, and could have been coming from atypical material.

Cenchrus ciliaris L. (synonym *Pennisetum ciliare* (L.) Link) is an intermediate species between *Cenchrus* and *Pennisetum*. It is an excellent perennial fodder grass, and has been the subject of several embryological studies. Fisher et al. (1954) and Sherwood et al. (1994) found it to be a facultative apomict, though highly aposporic, with four ploidy levels, 2n = 36, 32, 40 and 54, indicating a basic chromosome number of x = 9. Multiple embryo sacs (polyembryony) were regularly observed. Snyder et al. (1955) confirmed these findings, and also found that the species is pseudogamic. Taliaferro & Bashaw (1966) and later Sherwood et al. (1994) studied the inheritance of obligate apomixis of *C. ciliaris*, after the discovery of a biotype with a high level of sexuality (Bashaw, 1962). Extensive selfing and crossing experiments in apomictic and sexual tetraploids showed that the data fit a two locus model (Figure 2) for tetrasomic transmission, with a dominant allele (B) in one locus for sexuality, and another dominant allele (A) for apospory, on another locus, and which is hypostatic to B (Sherwood et al., 1994). Sexual parents thus would have the genotypes aaaabbbb, AaaaBbbb, AAaaBbbb, AAAaBbbb, or AAAABbbb, while the aposporous parents would have the genotypes Aaaabbbb, AAaabbbb, AAAabbbb, or AAAAbbbb. Crosses between *P. glaucum* and different wild apomictic species of *Pennisetum*, especially *P. squamulatum* and *P. orientale*, in order to transfer resistance of apomixis genes into *P. glaucum*, have been subject of several breeding programs, often with success (Patil & Singh, 1964; Dujardin & Hanna, 1983a, b, 1984a, c, 1985a, b, 1986, 1987, 1988, 1989a, b, 1990; Mohindra & Minocha, 1991; Busri & Chapman, 1992; Hanna, 1979; Hanna & Dujardin, 1982, 1986, 1990; Hanna et al., 1989, 1993; Ozias-Akins et al., 1989, 1993). Crosses between hexaploid *P. pedicellatum* or *P. polystachion* with diploid or tetraploid pearl millet resulted in partial seed development with the diploid pearl millet, so that embryo culture might be a tool for recovering these hybrids (Dujardin & Hanna, 1989). Mutagene treatments with X-rays in *P. pedicellatum* (Saran & Narain, 1981), as well as treatments with other crops and other mutagens, in order to break through the apomictic barrier, had no effect on the mode of reproduction, but changed at most the morphology. Lubbers et al. (1994) analyzed 11 apomictic and 8 sexual *Pennisetum* species and found that two molecular markers, a RAPD and a RFLP/STS, were specific for the apomicts. The RAPD marker was associated with 3 species, the RFLP/STS marker with 8 species, the last one evaluated to be more closely linked to the apomixis gene(s), neither of them though with species of section *Brevivalvula*, *P. pedicellatum*, *P. polystachion* and *P. subangustum*.

Spikelet proliferation

Agamospermy, as described above, is the common way of reproduction in *Pennisetum* section *Brevivalvula*. Another form of asexual reproduction found in this section and related with the inflorescence, is vivipary. Several terms have been used to describe the phenomenon of 'the conversion of the spikelet, above the two glumes, into a leafy shoot' (Arber, 1934) in grasses; vegetative proliferations (Arber, 1934), vivipary (Brown & Emery, 1958) and bulbil formation (Nair & Pillai, 1969; Pantulu, 1969) are frequently encountered. The main characteristic of these spikelets is that they are sterile and the proliferations develop without seed formation. Gustafsson (1946), followed by Nygren (1949), prefers the term vivipary, while the propagules exist of bulbils or bulblets. They distinguish several groups of vivipary, one of which is the vegetative shoot formation in the inflorescences of grasses, especially in *Agrostis*, *Deschampsia*, *Festuca* and *Poa*. In Britain, Wycherley (1954a) makes a distinction between viviparous races and occasional vegetatively proliferating plants. In viviparous races the leafy proliferation is always formed as a hereditary characteristic, it becomes detached and serves to propagate the plant and is not modified by environmental influences. Humidity is often necessary though for the detached plants to establish themselves. An exception is *Poa bulbosa* L. var. *vivipara* Koel. which is proliferating vegetatively under dry conditions, with the bulbils surviving because they are succulent. Spikelet prolifera-

tion in plants which are not members of the viviparous races is not hereditary and occurs in the temperate zone when the day length is decreasing, or under greenhouse conditions, when there is insufficient vernalization. In this case Wycherley (1954b) prefers the older and more accurate term proliferation, while he dismisses bulbil formation as being non satisfactory, as it is applied to plants which wear bulbils in parts other than the inflorescence. Arber (1934) prefers the term vivipary to be used to germination of undetached seeds only.

In the genus *Pennisetum*, Nair & Pillai (1969) report bulbil formation for the first time, in hexaploid *P. polystachion*. The proliferations exist here of two to three well developed leaves, are surrounded by the involucre and are rootless; and when planted in the soil, they failed to develop normally. They suggested that the bulbils develop by modification of the spikelets into vegetative buds. Pantulu (1969) observed vegetative structures that looked like bulbils on the inflorescences of hexaploid *P. pedicellatum* plants. They were neither observed on the tetraploid race, nor on the tetraploid or hexaploid race of *P. polystachion*. He transplanted fifty of these proliferated spikelets when they obtained their maximum size and more than 50% of these plantlets grew into mature plants.

Spikelet proliferation has been observed by me in *P. polystachion* and *P. subangustum* originating from central Benin and in *P. setosum* originating predominantly from the south of Benin, a few coming from Côte d'Ivoire. These observations have been made in Niger, under experimental conditions, from seeds collected from the regions mentioned (Renno et al., 1995). In section *Brevivalvula* vivipary occurs in polyploid taxa: the *P. polystachion* and *P. subangustum* samples are tetraploid, the *P. setosum* sample is hexaploid. As for the survival of these proliferations, tests in which individual proliferations were transplanted in pots always failed to produce plants, while when parts of inflorescences with the proliferations still attached were put in the soil, roots would be formed, and plants would develop normally. Sometimes these vegetative proliferations would develop tiny inflorescences, while they were still attached to the inflorescence themselves, and in which normal seed developed, which were viable, and produced plants genetically identical to the mother, as was tested through electrophorestical analysis (non published data).

As Arber (1934) states, vivipary is easiest to find on plants grown during the rainy season, which indicates a dependence on external conditions, but the fact that the proliferations occur only on plants of certain origins, also indicates a hereditary characteristic. He observed that in *Festuca ovina* L. a normal, sexual form was diploid, but plants that formed only vegetative proliferations were hexaploid (2n = 42).

Uses of section *Brevivalvula*

Fodder quality

Most *Brevivalvula* species are browsed by cattle passing through fallow land and along roads and villages. Especially *P. pedicellatum* and *P. setosum* are promising species for improving grass land quality and have been evaluated since the fifties in several countries, especially in India and Fiji. Because of its annual life cycle, *P. pedicellatum* is only suitable for temporary pastures (Whyte, 1964; Singh & Katoch, 1980), and it serves at the same time as a soil stabilizer (Bhag Mal et al., 1980) in the drier zones of India.

P. pedicellatum can stand several cuts a year for green fodder, and is generally used as a cut-and-carry green forage at ear emergence (Whyte, 1964; Skerman & Riveros, 1990) but it can be made into silage and hay (Bartha, 1970). It grows well in mixtures (Skerman & Riveros, 1990) or in rotation cropping with fodder legumes (Whyte, 1964). As a short rotation forage crop with maize or groundnuts it yields better than traditional forage grasses, especially when fertilized (Chatterjee et al., 1974), while the roots and stubbles also increase the soil fertility.

Singh & Prasad (1980) concluded on the basis of a comparative study of 38 *P. pedicellatum* genitors, that superior genotypes for fodder yield can be obtained only if selection is focused on tiller number, leaf length, leaf number and stem girth, while Singh & Arora (1970) add time of flowering and disease resistance to this list. When comparing the green fodder yield of different *P. pedicellatum* cultivars with *Sorghum bicolor* (Singh & Arora, 1970), or with other *Pennisetum* species and crosses (Singh & Katoch, 1980; Hanna et al., 1989) the species invariably is among the best performers. The study of Chatterjee & Kumar (1964) concerned 25 so-called *P. pedicellatum* strains, which were compared for their time of flowering, seed-set and green fodder yield. However, on the basis of the description of the inflorescences and photographs, they are more likely to be a mixture of three species, *P. pedicellatum* (19 strains), *P. setosum* (1 strain, perennial, originating from Australia), and *P. subangustum* (5 strains).

The combined morphological and cytological characteristics of different biotypes of *P. pedicellatum* have been subject to many evaluations, in order to find types with a superior character set for fodder improvement. Hexaploid races were often found to perform better than the tetraploid races, but there is a large variability in economic traits. Yadav et al. (1980) and Sharma et al. (1980) found that the hexaploids flowered later, the culms were thicker and they had more and bigger leaves than the tetraploids but there were no differences between plant height, tiller number and dry matter yield. Patil & Singh (1980) and Bhag Mal et al. (1980) concluded that hexaploids in general were taller, had more tillers, a higher sugar and protein content and a higher yield than the tetraploids. However, the clustering pattern of 36 varieties did not follow their geographic distribution strictly (Bhag Mal et al., 1980), indicating other selection pressures than geographical isolation. Other studies were focused on relationships between the morphology and ploidy levels of different biotypes of *P. pedicellatum* (Chatterji & Das, 1979; Chatterji & Sahu, 1982), and it seems that biotypes based on morphology only, can contain different chromosomal races.

P. setosum is cultivated in India, Thailand and the Fiji islands. Partridge (1975) uses the name *P. polystachion*, or mission grass, but from specific characteristics mentioned like poor tillering capacity, tussucky nature, height of 2 metres and greenness at the base of the plant during the dry season, rather indicate the perennial species *P. setosum*. The species has spread throughout the drier areas of Fiji, after its introduction in the 1920s. It does not persist under heavy grazing and after flowering the stems lignify and become inedible. It makes a useful hay though if cut before maturity, but is usually cut and fed green to cattle in India, as well as in Thailand and Fiji. In Fiji *P. polystachion* is also used in intercropping trials with forage legumes (Partridge, 1975) or other fodder grasses (Roberts, 1970). In Uganda, Eggeling (1947) describes *P. polystachion* as a perennial fodder plant, so he probably means *P. setosum* as well. It provides a good bulk of fodder for two years, but is only liked by cattle when it is young. He concludes that there are probably a number of strains, some palatable, others not.

Resistance for pests and diseases

When species are being evaluated for their fodder quality, it is equally important for them to be resistant to pests and diseases, partly so that introductions do not become hosts for these pests, and partly because this resistance might be transferable to cultivated crops.

P. polystachion and four other widespread African grasses have been evaluated as host plants for two maize stem borers, *Sesamia calamistis* Hampson and *Eldana saccharina* Walker, under laboratory conditions, after they have been recurrently reported as hosts. The survival rate of the larvae on these grasses was very low, less than 10% for *S. calamistis* and less than 5% for *E. saccarina*, compared to an artificial diet, resp. 95% and 60%, or maize, resp. 30% and 19% (Shanower et al., 1993). The survival rate of the larvae on four grasses was actually close to 0%, only on *Sorghum arundinaceum* (Desv.) Stapf some larvae survived (5–10%), probably because of the relatively large stems. *P. polystachion* can therefore be disregarded as a suitable host for these two stemborers.

Wilson & Hanna (1992) studied the disease resistance of 98 wild *Pennisetum* accessions from the first gene pool and 27 from the tertiary gene pool of *Pennisetum*. The tertiary gene pool species were evaluated for resistance to six fungi species. All the species, including several accessions of *P. pedicellatum*, *P. polystachion* and *P. subangustum*, were resistant to *Puccinia substriata* var. *indica*. All species except *P. squamulatum* were resistant to *Pyricularia grisea* as well, even the only accession of *P. pedicellatum*, despite the results of Saikai et al. (1983), who found it to be susceptible, and listed the species as a new host. Reactions to the other fungi ranged from highly resistant to susceptible, so probably considerable differences exist among the provenances for disease resistance. Hoffman (1990) mentions *P. pedicellatum* as a host for a whole range of parasitic plants, in Mali: *Striga hermonthica* (Del.) Benth., *S. aspera* (Willd.) Benth., *S. passargei* Engl., *Buchnera hispida* Buch.-Ham., *Rhamphicarpa fistulosa* (Hochst.) Benth., *Cuscuta campestris* R. Br., and *Cassytha filiformis* L. In some preliminary studies on resistance of *P. pedicellatum*, *P. polystachion* and *P. hordeoides* to *Striga hermonthica* (Ngarossal & Warou, 1993; Sy, 1994; Koulengar, 1995) it was shown that differences in susceptibility to *Striga* do exist among the provenances, but also between accessions of a same provenance. This is conform the fact that many *Brevivalvula* species reproduce apomictically, and many genetically different clones exist.

Conclusions

In *Pennisetum* the classification of the taxa into 5 sections is mostly a matter of morphological likeness, and not based on genetic relationships. Only the relationships among taxa in section *Brevivalvula* or section *Penicillaria* seem to be based on more than morphology alone. Six morphological taxa have been recognized in *Brevivalvula*, based on the largest polymorphism found in the section in West Africa. The section has spread over most of the tropics successfully, but confusion exists on geographical distribution patterns due to incomplete herbarium material, synonymy, and the controversy on the life cycles of *P. polystachion* and *P. setosum*. Section *Brevivalvula* is a highly polyploid and agamic complex: 4 euploid and 12 aneuploid levels have been found until now, the polyploids being apomictic (facultative or obligate), the diploid *P. polystachion* and *P. subangustum*, sexual. Spikelet proliferation, an alternative form of asexual reproduction, has been observed in tetraploid *P. polystachion* and *P. subangustum*, and hexaploid *P. setosum*. *P. pedicellatum* and *P. setosum* have been evaluated as excellent fodder species, but more research needs to be done on pest and disease resistance, as some studies have shown the susceptibility of several taxa to *Striga hermonthica*.

In order to better understand the evolutionary processes active in the section, research will have to focus on identification of clones through electrophoretical and, more precise, ADN-chloroplast analyses in order to identify apomictic and sexual taxa. Other points of interest are clone formation in relation to morphology, polyploidy, apomixis and geographical distribution, reproduction plasticity of clones for forage production and the inheritance of apomixis genes in pearl millet (*P. glaucum*). These informations will help to determine as well which taxonomic ranks have to be attributed to the taxa, for the sake of an unequivocal identification.

Acknowledgements

I am indebted to my co-promotor Dr. J.-F. Renno from ORSTOM (Niger), whose useful comments are kindly acknowledged. I am very grateful to Ir. R. Tibeyrenc for his help to finalize the maps.

References

Amoukou, A.I. & L. Marchais, 1993. Evidence of a partial reproductive barrier between wild and cultivated pearl millets (*Pennisetum glaucum*). Euphytica 67: 19–26.

Arber, A., 1934. *Gramineae*: A study of cereal, bamboo, and grass. Cambridge University Press.

Asker, S.E. & L. Jerling, 1992. Apomixis in plants. CRC Press, Florida.

Bartha, R., 1970. Fodder plants in the Sahel zone of Africa. Afrika-Studien no. 48. Weltforum Verlag, München.

Bashaw, E.C., 1962. Apomixis and sexuality in buffelgrass. Crop Sci 2: 412–415.

Bhag Mal, B.D. Patil & M.S. Yadav, 1980. Gene pool and its classification in Dinanath grass. In: V.P. Gupta & J.L. Minocha (Eds.), Trends in Genet Res Pennisetums, pp. 275–278. Punjab Agric Univ, Ludhiana.

Birari, S.P., 1981a. Cytology of apomixis in *Pennisetum polystachion* Schult. J Maharashtra Agric Univ 6 (3): 205–208.

Birari, S.P., 1981b. Mechanism of apomixis in *Pennisetum polystachion* Schult. J Maharashtra Agric Univ 6 (3): 208–212.

Bor, N.L., 1960. Grasses of Burma, Ceylon, India and Pakistan. Pergamon Press, London.

Brown, W.V. & W.H.P. Emery, 1958. Apomixis in the *Gramineae: Panicoideae*. Am J Bot 45: 253–263.

Brunken, J.N., 1977. A systematic study of *Pennisetum* sect. *Pennisetum (Gramineae)*. Am J Bot 64 (2): 161–176.

Brunken, J.N., 1979a. Cytotaxonomy and evolution in *Pennisetum* section *Brevivalvula (Gramineae)* in tropical Africa. Bot J Lin Soc 79: 37–49.

Brunken, J.N., 1979b. Morphometric variation and the classification of *Pennisetum* section *Brevivalvula (Gramineae)* in tropical Africa. Bot J Lin Soc 79: 51–64.

Busri, N. & G.P. Chapman, 1992. Reproductive and isozyme variation in an unstable *Pennisetum* hybrid progeny. In: G.P. Chapman (Ed.), Desertified Grassland: Their Biology and Management, pp. 309–313. Linnean Society Symposium Series No. 13, Academic Press, London.

Carnahan, H.L. & H.D. Hill, 1961. Cytology and genetics of forage grasses. Bot Rev 27: 1–162.

Chase, A., 1921. The Linnaean concept of pearl millet. Am J Bot 8: 41–49.

Chase, A. & C.D. Niles, 1962. Index to grass species. Vol 3. G.K. Hall & Co.

Chatterjee, B.N. & A. Kumar, 1964. Inter-strain variations in *Pennisetum pedicellatum*. Indian Forester 90: 477–483.

Chatterjee, B.N., B. Roy & K.K. Bhattacharjee, 1974. *Pennisetum pedicellatum* as a short rotation fodder crop for the eastern region of India. J Soil Water Cons India 23: 47–53.

Chatterji, A.K. & A.P. Das, 1979. Cytomorphological studies of the biotypes of *Pennisetum pedicellatum* Trin. Caryologia 32 (1): 5–14.

Chatterji, A.K. & G.K. Pillai, 1970. Apomixis in *Pennisetum pedicellatum* Trin. Sci Cult 36: 667–669.

Chatterji, A.K. & N. Sahu, 1982. Biotypic differences in the karyology of *Pennisetum pedicellatum* Trin. Biol Plant (Praha) 24 (1): 13–19.

Chatterji, A.K. & D.H. Timothy, 1969a. Microsporogenesis and embryogenesis in *Pennisetum flaccidum* Griseb. Crop Sci 9: 219–222.

Chatterji, A.K. & D.H. Timothy, 1969b. Apomixis and tetraploidy in *Pennisetum orientale* Rich. Crop Sci 9: 796–799.

Chowdhury, M.K.U. & R.L. Smith, 1988. Mitochondrial DNA variation in pearl millet and related species. Theor Appl Genet 76: 25–32.

Clayton, W.D., 1972. *Gramineae*. 101. *Pennisetum*. In: F.N. Hepper (Ed.), Flora of West Tropical Africa (III), pp. 459–462. Crown Agents, London.

Clayton, W.D. & S.A. Renvoize, 1982. *Pennisetum*. In: R.M. Polhill (Ed.), Flora of Tropical East Africa, pp. 672–690. A.A. Balkema, Rotterdam.

D'cruz, R. & P.S. Reddy, 1968. Apomixis in *P. massaicum* Stapf. Sci Cult 34: 255–257.

Dujardin, M. & W.W. Hanna, 1983a. Apomictic and sexual pearl millet - *Pennisetum squamulatum* hybrids. J Hered 74: 277–279.

Dujardin, M. & W.W. Hanna, 1983b. Meiotic and reproductive behavior of facultative apomictic BC1 offspring derived from *Pennisetum americanum-P. orientale* interspecific hybrids. Crop Sci 23: 156–160.

Dujardin, M. & W.W. Hanna, 1984a. Cytogenetics of double cross hybrids between *Pennisetum americanum-P. purpureum* amphiploids and *P. americanum* - *P. squamulatum* interspecific hybrids. Theor Appl Genet 69: 97–100.

Dujardin, M. & W.W. Hanna, 1984b. Microsporogenesis, reproductive behavior, and fertility in five *Pennisetum* species. Theor Appl Genet 67: 197–201.

Dujardin, M. & W.W. Hanna, 1984c. Pseudogamous parthenogenesis and fertilization of a pearl millet - *Pennisetum squamulatum* apomictic derivative. J Hered 75: 503–504.

Dujardin, M. & W.W. Hanna, 1985a. Cytology and reproductive behavior of pearl millet-Napier grass hexaploids - *Pennisetum squamulatum* trispecific hybrids. J Hered 76: 382–384.

Dujardin, M. & W.W. Hanna, 1985b. Cytology and reproduction of reciprocal backcrosses between pearl millet and sexual and apomictic hybrids of pearl millet - *Pennisetum squamulatum*. Crop Sci 25: 59–62.

Dujardin, M. & W.W. Hanna, 1986. An apomictic polyhaploid obtained from a pearl millet - *Pennisetum squamulatum* apomictic interspecific hybrid. Theor Appl Genet 72: 33–36.

Dujardin, M. & W.W. Hanna, 1987. Inducing male fertility in crosses between pearl millet and *Pennisetum orientale* Rich. Crop Sci 27: 65–68.

Dujardin, M. & W.W. Hanna, 1988. Production of 27-, 28-, and 56-chromosome apomictic hybrid derivates between pearl millet (2n = 14) and *Pennisetum squamulatum* (2n = 54). Euphytica 38: 229–235.

Dujardin, M. & W.W. Hanna, 1989a. Crossability of pearl millet with wild *Pennisetum* species. Crop Sci 29: 77–80.

Dujardin, M. & W.W. Hanna, 1989b. Developing apomictic pearl millet – characterisation of a BC_3 plant. J Genet Breed 43: 145–151.

Dujardin, M. & W.W. Hanna, 1990. Cytogenetics and reproductive behavior of 48-chromosome pearl millet - *Pennisetum squamulatum* derivates. Crop Sci 30: 1015–1016.

Eggeling, W.J., 1947. An annotated list of the grasses of the Uganda protectorate. Government Printer, Uganda.

Fisher, W.D., E.C. Bashaw & E.C. Holt, 1954. Evidence for apomixis in *Pennisetum ciliare* and *Cenchrus setigerus*. Agron J 16 (9): 401–404.

Gould, F.W., 1965. Chromosome numbers in some Mexican grasses. Bol Soc Bot Mex 29: 49–62.

Gould, F.W. & T.R. Soderström, 1974. Chromosome numbers of some Ceylon grasses. Can J Bot 52: 1075–1090.

Griffiths, A.J.F., J.H. Miller, D.T. Suzuki, R.C. Lewontin & W.M. Gelbart, 1993. An introduction to genetic analysis. W.H. Freeman & Co., New York.

Groves, R.H., 1991. Weeds of tropical Australia. In: F.W.G. Baker & P.J. Terry (Eds.), Tropical Grassy Weeds, pp. 189–196. CASAFA Report Series No. 2, CAB, Wallingford.

Gustafsson, A., 1946. Apomixis in higher plants. Part I. The mechanism of apomixis. Lunds Univ Arssk Avd 2 (42): 1–66.

Hafliger, E. & H. Scholz, 1980. Grass weeds 1. Panicoid grass weeds. Documenta Ciba-Geigy, Basle.

Hanna, W.W., 1979. Interspecific hybrids between pearl millet and fountain grass. J Hered 70: 425–427.

Hanna, W.W. & M. Dujardin, 1982. Apomictic interspecific hybrids between pearl millet and *Pennisetum orientale*. Crop Sci 22: 857–859.

Hanna, W.W. & M. Dujardin, 1986. Cytogenetics of *Pennisetum schweinfurthii* Pilger and its hybrids with pearl millet. Crop Sci 26: 449–453.

Hanna, W.W. & M. Dujardin, 1990. Role of apomixis in building and maintaining genome combinations. In: G. Kimber (Ed.), Chromosome Engineering in Plants, pp. 112–117. Proceedings of the Second International Symposium, Columbia, Missouri.

Hanna, W.W., M. Dujardin & W.G. Monson, 1989. Using diverse species to improve quality and yield in the *Pennisetum* genus. Proceedings of the XVI International Grassland Congress, pp. 403–404. Nice.

Hanna, W.W., M. Dujardin, P. Ozias-Akins, E. Lubbers & L. Arthur, 1993. Reproduction cytology and fertility of pearl millet - *Pennisetum squamulatum* BC4 plants. J Hered 84 (3): 213–216.

Harlan, J.R., 1975. Classification of cultivated plants. In: J.R. Harlan (Ed.), Crops and Man, pp. 107–121. Madison, Wisconsin.

Hitchcock, A.S., 1936. Manuel of the grasses of the West Indies. Misc Publ 243, United States Government Printing Office, Washington.

Hitchcock, A.S., 1950. Manual of the grasses of the United States. Misc Publ 200, United States Government Printing Office, Washington.

Hoffman, G., 1990. Une nouvelle approche de l'étude des phanérogames parasites au Mali. Deuxieme séminaire sur la lutte intégré contre les ennemis des cultures vivrieres dans le Sahel, Bamako, 7 p.

Hrishi, N.J., 1952. Studies on the cytogenetics of six species of Pennisetums and their comparative morphology and anatomy. Genetica 26: 280–356.

Husain, S.N., Y. Saideswara Rao, V. Manga & M.V. Subba Rao, 1990. Chemotaxonomic studies in the genus *Pennisetum* L. Rich. by isozyme analysis. Beitr Biol Pfl 65: 211–222.

Jackson, G. & P.O. Wiehe, 1958. An annotated check list of Nyasaland grasses. The Government Printer, Zomba, Nyasaland.

Jauhar, P.P., 1981. Cytogenetics and breeding of pearl millet and related species. Alan R. Liss Inc., New York.

Joshi, A.B., B.D. Patil & P.L. Manchanda, 1959. Chromosome numbers in some grasses. Curr Sci 28: 454–455.

Kativu, S. & R. Mithen, 1988. *Pennisetum* in southern Africa. FAO/IBPGR Plant Gen Res Newslett 73/74: 1–8.

Khosla, P.K. & P.N. Mehra, 1973. IOPB chromosome number reports. XLI. Taxon 22: 650–651.

Koulengar, D., 1995. Le sensibilité de *Pennisetum polystachion* (L.) Schult. de différentes provenances du Sahel pour le *Striga hermonthica* (Del.) Benth. DFPV-AGRHYMET, Niamey, pp. 1–13.

Krishnaswamy, N. & V.S. Raman, 1949. A note on the chromosome numbers of some economic plants of India. Curr Sci 18: 376–378.

Krishnaswamy, N., V.S. Raman, B.V. Shetty & P. Chandrasekharan, 1954. Chromosome numbers of some Indian economic plants. Curr Sci 23: 64–65.

Koechlin, J., 1962. Flore du Gabon. V. Famille des graminées. Muséum National d'Histoire Naturelle, Paris.

Lagudah, E.S. & W.W. Hanna, 1989. Species relationship in the *Pennisetum* gene pool: enzyme polymorphism. Theor Appl Genet 78: 801–808.

Lagudah, E.S., & W.W. Hanna, 1990. Patterns of variation for seed proteins in the *Pennisetum* gene pool. J Hered 81 (1): 25–29.

Launert, E. & G.V. Pope, 1989. Flora Zambesiaca. Vol. 10, part 3. *Gramineae*. Flora Zambesiaca Managing Committee, London.

Le Bourgeois, T. & H. Merlier, 1995. Adventrop. Les adventices d'Afrique soudano-sahélienne. CIRAD-CA, Montpellier.

Lebrun, J.-P. & A.L. Stork, 1995. Enumération des plantes à fleurs d'Afrique tropicale. Vol. III – Monocotylédones: *Limnocharitaceae* à *Poaceae*. Conservatoire et Jardin Botaniques de la Ville de Genève, Genève.

Lonsdale, W.M. & A.M. Lane, 1994. Tourist vehicles as vectors of weed seeds in Kakadu national park, northern Australia. Biol Cons 69: 277–283.

Lubbers, E.L., L. Arthur, W.W. Hanna & P. Ozias-Akins, 1994. Molecular markers shared by diverse apomictic *Pennisetum* species. Theor Appl Genet 89: 636–642.

Luces de Fèbres, Z., 1963. Las gramineas del distrito federal. Instituto Botanico, Caracas.

Maillet, J., 1991. Control of grassy weeds in tropical cereals. In: F.W.G. Baker & J. Terry (Eds.), Tropical Grassy Weeds, pp. 112–143. CASAFA Report Series No. 2, CAB, U.K.

Mehra, P.N., P.K. Khosla, B.L. Kohli & J.S. Koonar, 1968. Cytological studies in northern Indian grasses (Part 1). Res Bull Panjab Uni 19: 157–230.

Mehra, P.N. & P. Remanandan, 1973. Cytological investigation in West Himalayan *Panicoideae*. Cytologia 38: 259–270.

Mitra, K. & N. Datta, 1967. IOPB chromosome number reports. XIII. Taxon 16: 445–461.

Mohindra, V. & J.L. Minocha, 1991. Pollen pistil interactions and interspecific incompatibility in *Pennisetum*. Euphytica 56: 1–5.

Muniyama, M. & K.N. Narayan, 1975. IOPB chromosome number reports. XLVIII. Taxon 24 (2/3): 367–372.

Nair, V.G. & P.K. Pillai, 1969. Bulbism in *Pennisetum polystachyon*. Agric Res J Kerala 6: 54.

Naithani, S.P. & K.P. Sisodia, 1966. Preliminary meiotic study in *Pennisetum pedicellatum* Trin. Curr Sci 35: 343–344.

Napper, D.M., 1965. Grasses of Tanganyika. Bulletin No. 18. Ministry of Agriculture, Forests and Wildlife, Tanzania.

Narayan, K.N., 1955. Cytogenetic studies of apomixis in *Pennisetum*. Proc Indian Sci 41: 196–208.

Nath, J. & M.S. Swaminathan, 1957. Chromosome numbers of some grasses. Indian J Genet Plant Breed 17: 102.

Nath, J., M.S. Swaminathan & K.L. Mehra, 1971. Cytological studies in the tribe *Paniceae, Gramineae*. Cytologia 35: 111–131.

Ngarossal, N. & M. Warou, 1993. Effet de l'engrais azoté sur l'émergence et le développement du *Striga hermonthica* (Del.) Benth. sur les espèces sauvages et cultivées de *Pennisetum* en pots. DFPV-AGHRYMET, Niamey, pp. 1–20.

Nogler, G.A., 1984. Gametophytic apomixis. In: B.M. Johri (Ed.), Embryology of Angiosperms, pp. 475–518. Springer Verlag, New York.

Nygren, A., 1949. Studies on vivipary in the genus *Deschampsia*. Hereditas 15: 27–32.

Nyoka, G.C., 1982. The influence of fallow period on weed vegetation and rice fields in Sierra Leone. Trop Pest Manag 28 (1): 1–9.

Olorode, O., 1974. Chromosome counts in some Nigerian grasses. Cytologia 39: 429–435.

Olorode, O., 1975. Additional chromosome counts in Nigerian grasses. Brittonia 27: 63–68.

Ozias-Akins, P., M. Dujardin, W.W. Hanna & I.K. Vasil, 1989. Quantitative variation recovered from tissue cultures of an apomictic interspecific *Pennisetum* hybrid. Maydica 34: 123–132.

Ozias-Akins, P., E.L. Lubbers, W.W. Hanna & J.W. McNay, 1993. Transmission of the apomictic mode of reproduction in *Pennisetum*: co-inheritance of the trait and molecular markers. Theor Appl Genet 85: 632–638.

Pantulu, J.V., 1969. Meiosis in two polymorphic species of *Pennisetum*. Curr. Sci 38: 122–123.

Partridge, I.J., 1975. The improvement of Mission grass (*Pennisetum polystachyon*) in Fiji by topdressing superphosphate and oversowing a legume (*Macroptilium atropurpureum*). Trop Grasslands 9(1): 45–51.

Patil, B.D. & A. singh, 1964. An interspecific cross in the genus *Pennisetum* involving two basic numbers. Curr Sci 33: 255.

Patil, B.D. & A. Singh, 1980. Genetic and cytogenetic improvement of *Pennisetum* and its allied species for grassland and pasture production. In: V.P. Gupta & J.L. Minocha (Eds), Trends in Genetic Resources of Pennisetums, pp. 110–122. Punjab Agric Univ, Ludhiana, India.

Patil, B.D., A. Singh & R. Ghosh, 1964. Nature of ploidy in the pasture grass *Pennisetum ciliare* Linn. Curr. Sci 6: 184–185.

Pohl, R.W., 1980. Flora Costaricensis. Family No. 15, *Gramineae*. In: W. Burger (Ed.), Fieldiana Botany, pp. 462–463. Field Museum of Natural History, USA.

Pohl, R.W. & G. Davidse, 1971. Chromosome numbers of costa Rican grasses. Brittonia 23: 293–324.

Purseglove, J.W., 1972. Tropical crops. Monocotyledons. Longman, UK. Rangasamy, S.R.S., 1972. Cytological studies on diploid and polyploid taxa of the genus *Pennisetum*. Rich. Genetica 43: 257–273.

Rattray, J.M. 1960. Tapis graminéens d'Afrique. Collection FAO: Production végétale et protection des plantes, No 9. Etudes agricoles de la FAO, No 49. FAO, Rome.

Read, J.C. & E.C. Bashaw, 1969. Cytotaxonomic relationships and the role of apomixis in speciation in buffelgrass and birdwoodgrass. Crop Sci 9: 805–806.

Renno, J.-F., G.H. Schmelzer & J.H. de Jong, 1995. Variation and geographical distribution of ploidy levels in *Pennisetum* section *Brevivalvula* (*Poaceae*) in Burkina Faso, Benin and southern Niger. Pl Syst Evol 198: 89–100.

Renno, J.-F. & T. Winkel, 1996. Phenology and reproductive effort of cultivated and wild forms of *Pennisetum glaucum* under experimental conditions in the Sahel: implications for the maintenance of polymorphism in the species. Can J Bot 74: 959–964.

Robert, T., R. Lespinasse, J. Pernès & A. Sarr, 1991. Gametophytic competition as influencing gene flow between wild and cultivated forms of pearl millet (*Pennisetum typhoides*). Genome 34: 195–200.

Roberts, O.T., 1970. A review of pasture grasses in Fiji. I. Grasses. Trop Grassl 4: 129–137.

Rose Innes, R., 1977. A manual of Ghana grasses. Surbiton, Surrey.

Saideswara Rao, Y., M.R. Raju, M.V. Subba Rao & V. Manga, 1991. Free aminoacid analysis and species relationships of the genus *Pennisetum* (L.) Rich. Beitr Biol Pfl 66: 157–164.

Saikai, U.N., K.C. Puzari & P.K. Dutta, 1983. *Pennisetum pedicellatum*, a new host of *Pyricularia grisea*. J. Mycol Plant Pathol 12: 237.

Saran, S. & P.D. Nairan, 1982. X-irradiation studies in *Pennisetum pedicellatum*. J Cytol Genet 18: 111–114.

Sarr, A., M. Sandmeier & J. Pernès, 1988. Gametophytic competition in pearl millet, *Pennisetum typhoides* (Burm.) Stapf & Hubb. Genome 30: 924–929.

Schmelzer, G.H. & J.-F. Renno, (in press). Genetic variation in the agamic species complex of *Pennisetum* section *Brevivalvula* (*Poaceae*) from West-Africa: ploidy levels and isozyme polymorphism. Euphytica.

Shanower, T.G., F. Schulthess & N. Bosque-Perez, 1993. The effect of larval diet on the growth and development of *Sesamia calamistis* Hampson (*Lepidoptera: Noctuidae*) and *Eldana saccharina* Walker (*Lepidoptera: Pyralidae*). Insect Sci Appl 14 (5/6): 681–685.

Shanthamma, C. & K.N. Narayan, 1977. Formation of nucellar embryos with total absence of embryosacs in two species of Gramineae. Ann Bot 41: 469–470.

Sharma, C.M., P.K. Sinha & A.P. Singh, 1980. Cytomorphological studies in *Pennisetum pedicellatum*. In: V.P. Gupta & J.L. Minocha (Eds.), Trends in Genetic Resources of Pennisetums, pp. 205–207. Punjab Agric Univ, Ludhiana.

Sherwood, R.T., C.C. Berg & B.A. Young, 1994. Inheritance of apospory in buffalograss. Crop Sci 34: 1490–1494.

Simpson, C.E. & E.C. Bashaw, 1969. Cytology and reproductive characteristics in *Pennisetum setaceum*. Am J Bot 56: 31–36.

Singh, M. & W.D. Arora, 1970. Introduction and evaluation of *Pennisetum pedicellatum* as a summer fodder, pp. 621–624. Proc. 11th Int. Grassl Congress, Surfers Paradise, Australia.

Singh, D.N. & M.B.E. Godward, 1960. Cytological studies in the *Gramineae*. Heredity 15: 193–197.

Singh, L.N. & D.C. Katoch, 1980. Genetic diversity in *Pennisetum* species and their utilisation in meadows and partures of hills. In: V.P. Gupta & J.L. Minocha (Eds.), Trends in Genetic Resources of Pennisetums, pp. 267–273. Punjab Agric Univ, Ludhiana.

Singh, A.P. & B. Prasad, 1980. Component analysis of herbage yield in *Pennisetum pedicellatum*. In: V.P. Gupta & J.L. Minocha (Eds.), Trends in Genetic Resources of Pennisetums, pp. 251–254. Punjab Agric Univ, Ludhiana.

Sisodia, K.P.S., 1970. Cytological studies on some species in the genus *Pennisetum*. Theor Appl Genet 40: 26–31.

Sisodia, K.P.S. & R.N. Raut, 1980. Meiotic behaviour and fertility of hexaploid *Pennisetum pedicellatum* Trin. In: V.P. Gupta & J.L. Minocha (Eds.), Trends in Genetic Resources of Pennisetums, pp. 215–216. Punjab Agric Univ, Ludhiana.

Skerman, P.J. & F. Riveros, 1990. Tropical grasses. FAO Plant Production and Protection Series no. 23. Rome.

Snyder, L.A., A.R. Hernandez & H.E. Warmke, 1955. The mechanism of apomixis in *Pennisetum ciliare*. Bot Gaz 116: 209–221.

Stancioff, A., M. Staljanssens & G. Tappan, 1986. Cartograpie et télédetection des ressources de la République du Sénégal. Etude de la géologie, de l'hydrologie, des sols, de la végétation et des potentiels d'utilisation des sols. Direction de l'aménagement du territoire du Sénégal, U.S.A.I.D., Remote Sensing Institute, Sénégal.

Stanfield, D.P., 1970. Grasses. In: D.P. Stanfield & J. Löwe (Eds.), The Flora of Nigeria. Ibadan Univ. Press, Ibadan.

Stapf, O. & C.E. Hubbard, 1934. *Pennisetum*. In: D. Prain (Ed.), The Flora of Tropical Africa. Vol. IX, pp. 954–1070. Reeve & Co. Ltd., Ashford, Kent.

Subba Rao, M.V., D.M. Sujatha, Y. Saideswara Rao & V. Manga, 1988. Chemotaxonomic characters in twelve species of the genus *Pennisetum* (*Poaceae*). Proc Indian Acad Sci (Plant Sci) 98 (2): 111–120.

Sy, M., 1994. La sensibilité pour le *Striga hermonthica* (Del.) Benth. des clones de *Pennisetum pedicellatum* de différentes provenances du Sahel. DFPV-AGRHYMET, Niamey, pp. 1–14.

Sybenga, J., 1968. Cytogenetica. A. Oosthoek's Uitgeversmaatschappij, Utrecht.

Taliaferro, C.M. & E.C. Bashaw, 1966. Inheritance and control of obligate apomixis in breeding buffelgrass, *Pennisetum ciliare*. Crop Sci 6: 473–476.

Tateoka, T., 1965. Chromosome numbers of some grasses from Madagascar. Bot Mag Tokyo 78: 306–311.

Terry, P.J., 1991. Grassy weeds – a general overview. In: F.W.G. Baker & P.J. Terry (Eds.), Tropical Grassy Weeds, pp. 5–38. CASAFA Report Series No. 2, CAB, Wallingford.

Tjitrosoedirdjo, S.S., 1990. *Pennisetum polystachyon* (L.) Schult. Weed Info Sheet, SEAMO BIOTROP 3: 2.

Van der Zon, A.P.M., 1992. Graminées du Cameroun, Volume II. Flore, pp. 329–346. Wageningen Agricultural University Papers, Wageningen.

Veyret, Y., 1957. Les chromosomes somatiques chez quelques espèces de *Pennisetum*. Agron Trop 12 (5): 595–598.

Vishnuvardhan, Z. & N. Laksmi, 1989. Cytomorphological studies in two new biotypes of *Pennisetum pedicellatum* Trin. Cytologia 54: 73–78.

Watson, L. & M.J. Dallwitz, 1992. The grass genera of the world, pp. 674–676. CAB International, Wallingford.

Webster, R.D., 1987. The Australian *Paniceae* (*Poaceae*). Cramer, Berlin, Stuttgart.

White, F., 1986. La végétation de l'Afrique. ORSTOM-UNESCO, Paris.

Whyte, R.O., 1964. The grassland and fodder resources of India. Indian Counc for Agric Res (ICAR), New Delhi.

Wilson, J.P. & W.W. Hanna, 1992. Disease resistance in wild *Pennisetum* species. Plant Dis 76: 1171–1175.

Wycherley, P.R., 1954a. Vegetative proliferation of floral spikelets in British grasses. Ann Bot 18: 199–227.

Wycherley, P.R., 1954b. Proliferation of spikelets in British grasses. I. The taxonomy of the viviparous races. Watsonia 13: 41–56.

Yadav, M.S., S.N. Zadoo, Bhag Mal & S.N. Tripathi, 1980. Chromosomal races of *Pennisetum pedicellatum* in relation to their economic traits. In: V.P. Gupta & J.L. Minocha (Eds), Trends in Genetic Resources of Pennisetums, pp. 209–213. Punjab Agric Univ, Ludhiana.