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Cytogenetic studies in the *Andropogon gayanus-Andropogon tectorum* Complex in Southwestern Nigeria

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Abstract. The studies were carried on accessions of the *Andropogon gayanus-Andropogon tectorum* complex (Poaceae) in southwestern Nigeria to determine the chromosome numbers and meiotic dynamics in the species. This involves meiotic chromosome and pollen studies using standard procedures. Studies on the morphology and meiotic behaviour of collections of *A. gayanus* (2n = 40) and *A. tectorum* (2n = 20, 40) have been made. The cytogenetic studies show that the chromosome configuration of *A. gayanus* is a tetraploid (2n = 40) on a basic chromosome number of 10. *A. tectorum* occurs as a regular diploid on a chromosome number of 2n = 20 and it is the only species found in Ekiti State. Accession "Kiwani" was found to be a polyploid. *A. tectorum* with a chromosome number of 2n = 40. This study has also established the stability of the genome of the *Andropogon* complex. In spite of the occurrence of univalent and multiple associations, meiosis ensures a high percentage of pollen grains. The pollens of accession "Kiwani" (> 35 µm) were generally larger than those of other accessions while the other accessions of both *A. gayanus* and *A. tectorum* have modal pollen sizes less than 35 µm, although the *A. tectorum* accessions were generally smaller. The study concluded that the occurrence of the tetraploid (2n = 40 in accession AT10, "Kiwani" can be attributed to apomixis occurring in a lonely plant.

Keywords: *Andropogon gayanus, Andropogon tectorum*, Apomixis, "Kiwani", meiotic study.

INTRODUCTION

The genus *Andropogon* Linn., is a fairly large genus of the grass family, Poaceae, belonging to the tribe Andropogoneae (Hutchinson and Dalziel 1972; Olorode, 1984)). *Andropogon* is a pantropical genus of grasses of about 29 species almost confined to the tropical and warm temperate regions of the world, frequently forming an important part of the savanna vegetation in the tropics. The genus is composed of annual and perennial species frequently with tall culms, and leaf blades which can be linear to lanceolate or ovate. *Andropogon* is represented by about 14 species in Nigeria (Lowe 1989), although Stanfield (1970) had reported about 12 species.

The spikelets occur in pairs at each node of the raceme, each pair consisting of a pedicellate and a sessile spikelets. The sessile spikelet is bisexual while the pedicellate is unisexual male (Hutchinson and Dalziel 1972). The spikelets are articulated in such a way that at maturity, their pedicel and internodes all break apart leaving no central inflorescence stalk. The sessile spikelet bears a prominent awn which is flexed at an angle to the vertical axis of the glumes. A distinct colour difference exists between the two arms of the awn (Clayton 1969; Stanfield 1970).

Andropogon gayanus Kunth is a tall, tufted perennial grass that grows taller than 3 m. It has many tillers and abundant foliage especially during the rainy season (Chlleda and Crowder 1982). It forms a significant part of the vegetation of many savanna areas throughout Africa south of the Sahara, including South Africa. It is a polymorphic species. In Nigeria, four main varieties were recognized (Clayton, 1962). These are: var. *gayanus* (var. *genius*) Hack; var. *bisquamulatus* (Hochst) Hack var. *squamulatus* (Hochst) Stapf and var. *tridentatus*. Bowden (1963) considered var. *tridentatus* as split from var. *bisquamulatus* thus recognizing only three varieties.

A. gayanus is widespread and abundant in the Northern and Southern Guinea Savanna as well as in the drier areas of the derived savanna whereas *A. tectorum* occupies vast areas in the derived savanna, preferring moderate shade (Stanfield, 1970). However, certain areas in the derived savanna support the growth of both species equally well (Okoli and Olorode 1983). *Andropogon gayanus* is propagated by seeds, which are broadcasted or planted in rows and vegetatively by splitting the tufts. It is relatively free of major pests and diseases and is resistant to grazing and burning. These make it a useful grass for supporting a large number of ruminant animals in Northern Nigeria. It is also one of the high-yielding grasses in West Africa (Bogdan. 1977; Pagot, 1993). The economic importance of *Andropogon gayanus* for livestock grazing is that it is very palatable when young and serves as basic materials for woven houses. *Andropogon gayanus* is a highly-productive grass, which increases fuel loads, produces intense, late dry season fires which seriously damage native woody species; it is also useful as forage in permanent pastures grazed by ruminants. The stems are used for thatching and, when flattened, for weaving coarse grass mats as well as sometimes being planted for erosion control and soil restoration.

Andropogon tectorum Schum. & Thonn. is a perennial grass; caespitose. Culms can be 200–300 cm long without nodal roots or with prop roots. Ligules are eciliate membrane or a ciliolate membrane, 1–2 mm long. Leaf blade base tapers to the midrib and bears false petiole. Leaf-blades are lanceolate; 30–45 cm long; 10 – 25 mm wide; flaccid; light-green, apex is acuminate. *Andropogon gayanus* and *A. tectorum* are important natural fodder grasses in Nigeria. They are also useful in crop rotation, thatching and mat-making (Bowden, 1963) and offer an interesting opportunity for ecological, cytogenetic and evolutionary studies.

There is paucity of information about the genetic studies of the *Andropogon gayanus-Andropogon tectorum* complex aside from the first attempts by Okoli (1978). Further investigation of the precise nature and extent of the apomicitic phenomenon in these species would be both interesting and worthwhile.

MATERIALS AND METHODS

Field trips for plant collections covered agro-ecological zones of the following states: Osun, Ondo, Ogun, Oyo and Ekiti as shown in Figure 1. Whole plants of *Andropogon gayanus* and *Andropogon tectorum* were collected from different locations in Southwest, Nigeria. Accession numbers were given to the specimens. Seeds were also collected for planting and preservation. Garden populations were raised from the vegetative parts of some accessions and they were also maintained in the Botanical Garden of the Obafemi Awolowo University, Ile- Ife, Osun State. The accessions were nurtured to maturity and used for this study. Table 1 shows the locations, coordinates, descriptions of site and collectors of the accessions.

Footnote on Kiwani, this lone plant was discovered on a road side in a gravelly location, the three colleagues on the trip agreed on its pronounced gigas attributes suggesting polyploidy. This was a surprise in a region dominated by diploid *Andropogon tectorum*. After the arguments that ensued, the leader of the trip named the accession *KIWANI* which translates into "what else can this be?' It is denoted as AT10 too in part of the manuscript.

Meiotic chromosome studies

The young flower buds for meiotic chromosome study were collected between 9:00 am and 12:00 noon when the cell activities are believed to be at the peak (Jackson 1962) and stored in 1:3 Acetic acid: Ethanol. The anthers were removed, squashed and stained in FLP Orcein by the squashing technique described by Laose-

Figure 1. Map showing collection site.

bikan and Olorode (1972). The Pollen Mother Cells were examined and scored for chromosome associations. Good meiotic chromosome spreads were photographed at X100 objective under BK Series (Phase Contrast Microscope (PW-BK 5000T) equipped with a DCM 510 5 Megapixel Camera.

Pollen studies

Pollen stainability studies were carried out to assess the fertility of the accessions as well as the pollen size.

Table 1. Accessions of *Andropogon gayanus* (Kunth) - *Andropogon tectorum* (Schum & Thonns) studied and their sources.

Accn	Locations	Coordinates	Descriptions of site	Collectors
AG 1	Asawo, Oyo State	N 08° 59.848` E 04° 17.836`	Ruderal location, regular regrowth forest	Ojo, Faluyi, Azeez and Abraham
AG 2	Budo-Ode, Oyo State	N 08° 20.420` E 04° 14.039`	Derived Savanna	”
AG 3	Between Ogbomosho and Oko, Oyo State	N 08° 59.854` E 04° 17.835`	Ruderal location, regular regrowth forest	”
AG 4	Igbeti 1, Oyo State	N 08° 24.722` E 04° 15.467`	Dry water course, populated by heavy mat of grasses and sedges; chimeric lawn	”
AG 5	Igbeti 2, Oyo State	N 08^0 24.723` E $04^0$ 15.467`	Dry water course, populated by heavy mat of grasses and sedges; chimeric lawn	”
AG 6	Ogbomosho, Oyo State	N 08° 34.794` E 04° 14.669`	Regular regrowth forest with the presence of multiple grass species	”
AT 1	OAUTHC Road, Osun State	N 07° 30.870` E 04° 33.065`	Ruderal location with dwarf morphotypes propagating from crevices	Ojo, Faluyi and Nwokeocha
AT 2	O.A.U. Religious Centre, Osun State	N 07° 30.703` E 04° 33.065`	Ruderal on lateritic soil in company of other grasses, Asteraceae	”
AT 3	O.A.U. International School, Osun State	N 07° 31.793` E 04° 33.261`	Expanse of lateritic soil with close communities of *Andropogon tectorum*	”
AT 4	Ife-Ibadan road, Osun State	N 07° 22.774` E 04° 01.497`	At the fringe of road divider, surrounded by other grasses	Ojo and Faluyi
AT 5	Ondo road, Along Ore, Ondo State	N 07° 49.468` E 04° 52.444`	Ruderal on lateritic soil	Ojo
AT 6	Aladura, Ogun State	N 07° 30.068` E 04° 27.885`	Ruderal on lateritic soil	Ojo and Faluyi
AT 7	Omu-Ayede road, Ekiti State	N 07° 54.374` E 05° 20.167`	Ruderal location with a cluster of *Panicum maximum* and stands of *Chromolaena odorata*	Ojo, Faluyi, Matthew and Abraham
AT 8	Itaji-Oye Road, Ekiti State	N 07° 50.833` E 05° 20.661`	Ruderal location under a tree of *Parkia biglobosa* and *Alchornea laxiflora*	Ojo, Faluyi, Matthew and Abraham
AT 9	Ayede-Oye Road, Ekiti State	N 07° 50.438` E 05° 20.733`	Solitary plant, leaves are broad and usually short; in mesic location	”
AT 10	Erinmo Road, Ekiti State	N 07° 38.203` E 04° 51.755`	Ruderal location on lateritic soil in company of other grasses, Asteraceae	”

Accn: Accession, AG: *Andropogon gayanus*, AT: *Andropogon tectorum.*

Pollen stainability test

Matured pollen grains from each of the accessions were collected between 12:00 pm and 2:00 pm when the spikelets had opened. Pollens were dusted on microscope slides, stained with Cotton Blue in Lactophenol covered with cover slip and left for about 5 to 10 minutes for the pollen grains to properly take up the stain. Each prepared slide was viewed under a compound light microscope at x40 magnification. The pollens were scored as viable and non-viable using twenty fields for each of the accessions. Pollens that were well rounded, deeply-stained and moderately sized, were scored as viable. Those that were small–sized, irregularly-shaped and poorly-stained were scored as non-viable. Percentage pollen fertility were calculated using the formula below:

Pollen size distribution patterns

The diameter of one hundred (100) pollen grains were measured at random for each accession under the compound light microscope using graduated ocular micrometer at X40 objective magnification. Histograms were constructed to show the distribution pattern of the pollen sizes for all accessions.

RESULTS

Figures 4 to 6 show the main features of meiotic chromosomal studies in the accessions of *Andropogon gayanus* and *Andropogon tectorum* studied. In both *A. gayanus* and *A. tectorum* accessions studied, chromosome pairing was perfect in some of the Pollen Mother Cells. Some of the chromosome associations encoun-

Table 2. Morphological Features of the Accessions of *Andropogon gayanus-Andropogon tectorum* Studied.

Accn	Plant form	No. of leaves/ tiller	No. of tillers/ plant stand	Culm characteristics	Petiole
AG1	Broad leaves, heavy tillering, culm diameter fairly big. Plant type robust	6.45±0.15 (6 - 9)	32.85±6.09 (23–44)	Glabrous, green in colour covered with hairy leaf sheath.	Pubescent, grow up to 20 cm
AG2	Narrow leaves, heavy tillering, culm diameter thin. Plant type not so robust	6.33±0.14 (5 – 9)	34.50±5.79 (25-49)	"	Pubescent, grow up to 22 cm
AG3	Broad leaves, intermediate tillering, culm diameter fairly big. Plant type robust	6.20±0.23 (5 – 8)	25.45±8.50 (24-45)	"	Pubescent, grow up to 20 cm
AG4	Broad leaves, heavy tillering, culm diameter big. Plant type not so robust	6.35±0.16 (5–9)	31.23±6.09 (29-43)	"	Pubescent, grow up to 23 cm
AG5	Broad leaves, heavy tillering, culm diameter fairly big. Plant type robust	6.57±0.13 (5 – 9)	32.65±6.79 (27-47)	"	Pubescent, grow up to 22 cm
AG6	Broad leaves, heavy tillering, culm diameter big. Plant type robust	6.32±0.16 (5 – 8)	34.35±7.80 (23-51)	"	Pubescent, grow up to 28 cm
AT1	Narrow leaves intermediate tillering, culm diameter thin. Plant type stout	7.20±0.13 (5 – 9)	23.67±4.21 (26-43)	Glabrous, green in colour covered with hairless leaf sheath	Glabrous, grow up to 58 cm
AT2	Narrow leaves heavy tillering, culm diameter big. Plant type not so robust	7.31±0.21 (6 – 9)	31.33±7.88 (28-41)	Glabrous, green in colour covered with hairy leaf sheath	Glabrous grow up to 38 cm
AT3	Broad leaves, heavy tillering, culm diameter fairly big. Plant type robust	7.15±0.16 (5 – 8)	33.65±7.50 (27-40)	"	Glabrous grow up to 36 cm
AT4	Broad leaves, heavy tillering, culm diameter fairly big. Plant type robust	7.23± 0.13 (5 - 9)	31.75±6.85 (23-41)	Glabrous, purple in colour covered with hairy leaf sheath	Pubescent, grow up to 28 cm
AT5	Narrow leaves heavy tillering, culm diameter fairly big. Plant type robust	7.09±0.16 (6 – 9)	31.67± 3.72 (27-42)	Glabrous, purple in colour covered with hairless leaf sheath	Pubescent, grow up to 30 cm
AT6	Narrow leaves intermediate tillering, culm diameter fairly big. Plant type not so robust	7.12±0.15 (5 – 8)	29.50±5.65 (27-44)	Glabrous, green in colour covered with hairless leaf sheath	Glabrous, grow up to 30 cm
AT7	Broad leaves, heavy tillering, culm diameter big. Plant type robust	7.27±0.16 (6 – 9)	30.05±6.10 (21-45)	"	Glabrous, grow up to 28 cm
AT8	Broad leaves, heavy tillering, culm diameter fairly big. Plant type robust	7.40±0.16 (5 – 8)	32.54±5.08 (23-43)	Glabrous, green in colour covered with hairy leaf sheath	Glabrous, grow up to 22 cm
AT9	Broad leaves, heavy tillering, culm diameter big. Plant type robust	7.16±0.19 (5 – 9)	31.45±6.18 (21-42)	"	Glabrous, grow up to 26 cm
AT10	Broad, short leaves, very heavy tillering, culm diameter fairly big. Plant type robust	7.35±0.12 (6 - 8)	49.56±4.75 (39-69)	Glabrous, green in colour covered with hairless leaf sheath	Glabrous, grow up to 45 cm

Accn: Accession, AG: *Andropogon gayanus*, AT: *Andropogon tectorum*, No: Number.

tered were the formation of multivalents (especially in the polyploid accessions) for example formation of quadrivalents as chain of IV (Plates 4A and F), bivalents (frequently encountered) as ring II and rod II (Plates 5E and F) and occasionally occurrence of univalents in Plate 5E.

The following chromosomal configurations and aberrations were encountered in the meiotic chromosomes of the accessions studied: the formation of multivalents occurring especially in the polyploid accession, for instance, formation of quadrivalents resulting in a 5IV + 10II configuration as shown in Plate 4F, univalent resulting in 20I (Plate 5E), precocious movements at Anaphase I (Figure 4C). Normal bivalent pairing and regular segregation to the poles was also observed (Plate 4A and B). Table 3 shows the meiotic chromosome configuration of the accessions studied.

Pollen studies

Pollen stainability test

Generally, the pollen fertility in the accessions studied was high; it ranged from 83.47% to 97.20%. AT10, sample of the accession "Kiwani" collected on the Itawure-Erinmo Road (N 07°38.203` E04°51.755`) Ekiti State has the lowest value of 83.47% while accession AT1, collected along OAU-THC road (N 07°30.870` E 04°33.065`), Ile-Ife, Osun State has the highest value of 97.20% as shown in Table 4.

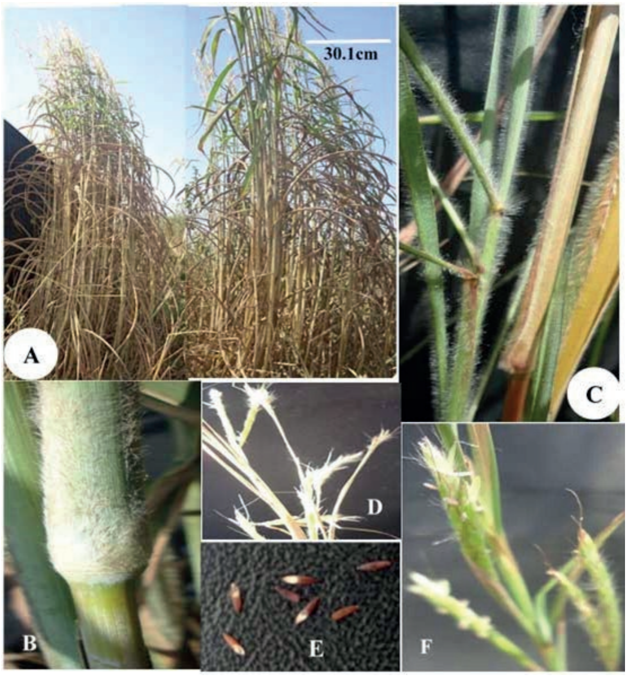

Figure 2. Morphological features of *Andropogon gayanus*. a: Plant form and adaptation; b: Internode; c: Hairy leaf sheath; d: Raceme pairs; e: Seeds; f: Spikelet.

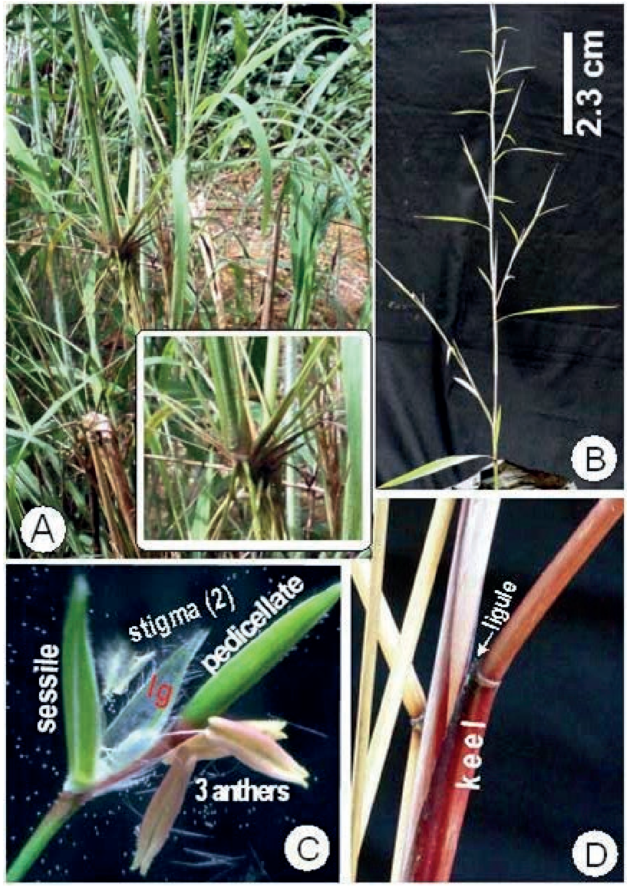

Figure 3. Morphological Features of *Andropogon tectorum*. a: Plant form and adaptation (Insect- Rooting at the node); b: Flowering Scape; c: Spikelet; d: The leaf showing sheath, keel and ligule; lg: Lower glume.

Pollen size distribution patterns

The pollens of AT10 "Kiwani", collected on the Itawure-Erinmo Road (N 07°38.203\` E 04°51.755\`) in Ekiti State had a majority falling in the large pollen size range while the other accessions of both AT and AG have modal pollen size having the highest frequency; although the AT accessions are generally smaller i.e. < 35 µm and the AG accessions are >35 µm as shown in Figures 7 and 8.

DISCUSSIONS

The key issues involved in occurrence of ploidy levels, meiotic studies within and among the two species of *Andropogon* studied can be summarized as follows:

1. two chromosome numbers were established: 2n = 40 in all accessions of *Andropogon gayanus* which paired as 20 II or at low levels of quadrivalents and univalents e.g. 2 IV + 16 II and 5 IV + 10 II. Segregation problems were very rare at Anaphase.

2. the dominant chromosome number in *Andropogon tectorum* is 2n = 20 which paired usually as 10 II, and occasionally, as 1 IV + 8II as in a AT4 collection from the Ife-Ibadan Road (N 07° 22.774\` E 04° 01.497\`), 20 I in AT9 accession from a location on the Ayede-Oye Road (N 07° 50.833\` E 05° 20.661\`) and 18 II + 4 I (2n = 40) in locality Kiwani, AT10 collected on a gravelly location on the Itawure-Erinmo Road (N 07° 38.203\` E 04° 51.755\`) both in Ekiti State, Nigeria.

The pairing patterns at diakinesis in *A. gayanus* suggests a diploid on a basic chromosome number of x = 20 paired as 20 II or an amphidiploid on a basic chromosome number of 10, while the regular occurrence of quadrivalent associations at low levels (2 IV+16 II, 5 IV + 10 II) suggest a tetraploid as a basic number of x = 10 with the four genomes still exercising considerable homology.

Okoli (1983) reported a chromosome number 2n = 40 for *Andropogon gayanus*, 2n = 20, 30 for *Andropogon tectorum* and their hybrids obtained by open and controlled crosses. The 2n = 20 chromosome in *A. tectorum* paired dominantly as 10 II and occasionally as 1 IV + 8 II which only occurred in a AT4 collection on

Table 3. Meiotic chromosome configurations (Diakinesis) in *Andropogon gayanus-Andropogon tectorum* accessions studied.

Serial No	Accn	Modal chromosome configuration	Diakinesis number
1	AG 1	5.05 ring II + 13.50 rod II	2n = 40
2	AG 2	4.10 ring II + 14.40 rod II + 1.45 Chain IV	“
3	AG 3	3.05 ring II + 14.20 rod II + 0.90 Chain IV	“
4	AG 4	4.55 ring II + 13.70 rod II	“
5	AG 5	3.05 ring II + 14.90 rod II + 1.15 Chain IV	“
6	AG 6	2.45 ring II + 11.90 rod II + 5.05 Chain IV	“
7	AT 1	4.95 ring II + 4.85 rod II	2n = 20
8	AT 2	4.85 ring II + 4.90 rod II	“
9	AT 3	4.95 ring II + 4.35 rod II + 0.45 Chain IV	“
10	AT 4	5.25 ring II + 4.25 rod II + 0.35 Chain IV	“
11	AT 5	4.80 ring II + 4.95 rod II	“
12	AT 6	7.05 ring II + 2.35 rod II	“
13	AT 7	6.85 ring II + 3.05 rod II	2n = 20
14	AT 8	4.05 ring II + 14.50 rod II	2n = 40
15	AT 9	0.95 ring II + 2.40 rod II + 6.45 I	2n = 20
16	AT 10	4.85 ring II + 7.05 rod II + 3.90 Chain IV + 1.90 I	2n = 40

Scores are based on 20 cells per accession.
Accn: Accession, AG: Andropogon gayanus, AT: Andropogon tectorum.

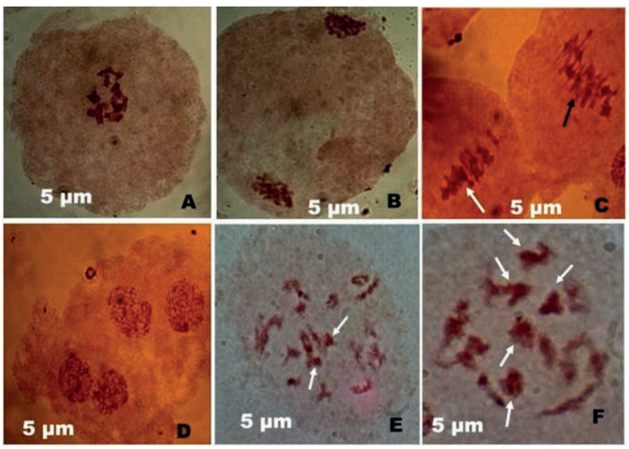

Figure 4. Chromosome Configurations in *A. gayanus* (2n = 40). A: AG 1, Metaphase I showing normal bivalent pairing as 20 II. B: AG 1, Telophase I showing clear segregations to the poles. C: AG 4, Late Metaphase I (white arrow, bottom cell) and Early Anaphase I (black arrow, top cell), showing precocious movements to the poles. D: AG 4, Tetrads of Telophase II. No laggard on restitution nuclei seen. E: AG 2, Diakinesis showing 2 IV + 16 II. White arrows show quadrivalents. F: AG 6, Diakinesis showing 5 IV + 10 II. White arrows show quadrivalents.

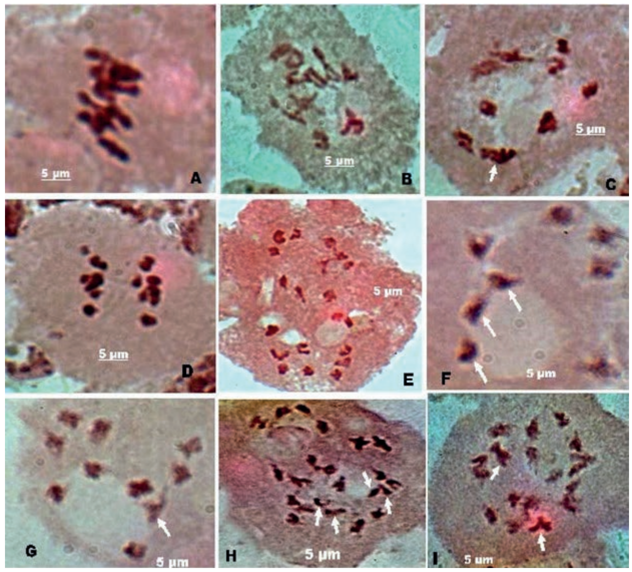

Figure 5. Chromosome configuration in the *A. tectorum* accessions (A-G: 2n = 20, H-I: 2n = 40). A: AT 1, Metaphase I showing normal bivalent pairing as 10 II. B: AT 2, Pachynema-Diplonema showing 10 II. C: AT 4, Diakinesis-Early Metaphase I showing 1 IV + 8 II. The white arrow shows a quadrivalent. D: AT 6, Anaphase I showing normal segregation to the poles. E: AT 9, Diakinesis showing 20 I. F: AT 7, Metaphase I showing three bivalents chromosomes around the nucleolus. G: AT 7, Late Diakinesis/Metaphase I showing 10 II. The white arrow probably shows the satellited pair. H: AT 10, Diakinesis showing 18 II + 4I. The white arrows indicate the four univalents. I: AT 10, Diakinesis showing 16 II + 2 IV. The white arrows indicate the two quadrivalents.

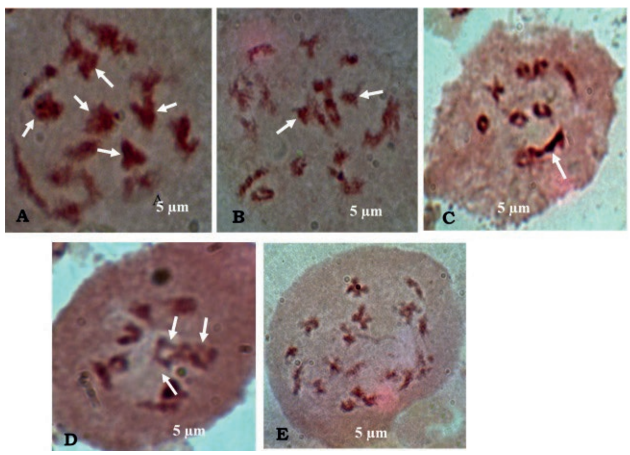

Figure 6. Chromosome Configurations for other accessions (A, B and E: 2n = 40, C and D: 2n = 20). A: AG 3, Diakinesis showing 5 IV + 10 II. White arrows show quadrivalents. B: AG 5, Diakinesis showing 2 IV + 16 II. White arrows show quadrivalents. C: AT 3, Diakinesis I showing 1 IV + 8 II. The white arrow shows a quadrivalent. D: AT 5, Diakinesis I showing fig. 8 and 9 II. White arrow showing fig. 8. E: AT 8, Diakinesis showing 20 II.

Table 4. Pollen size and fertility in the *Andropogon gayanus-Andropogon tectorum* accessions studied.

Characters				Pollen fertility		
Serial No	Accessions	Chromosome No	Mean ± S.D[a] (µm)	C.V. (%)	N[b]	%
1	AG1	2n = 40	43.24±4.75	11	1240	83.47
2	AG2	2n = 40	38.58±4.14	18	1892	87.53
3	AG3	2n = 40	41.25±4.91	12	1089	85.57
4	AG4	2n = 40	37.51±4.17	11	1068	96.34
5	AG5	2n = 40	36.95±4.09	11	1034	95.45
6	AG6	2n = 40	39.38±5.01	15	957	97.04
7	AT1	2n = 20	37.45±2.70	7	1098	96.45
8	AT2	2n = 20	36.52±2.82	7	1152	95.65
9	AT3	2n = 20	36.22±2.79	7	1068	95.77
10	AT4	2n = 20	36.38±2.57	7	1084	94.55
11	AT5	2n = 20	37.98±3.39	8	1194	93.13
12	AT6	2n = 20	37.75±3.23	9	1106	97.20
13	AT7	2n = 20	40.47±4.67	11	1278	95.85
14	AT8	2n = 40	41.95±4.43	12	1327	96.31
15	AT9	2n = 20	40.35±4.25	11	1285	93.54
16	AT10	2n = 40	41.59±4.57	12	1478	96.68

a: based on 100 measurements; b: number on which estimate was based; AG: *Andropogon gayanus*; AT: *Andropogon tectorum*; No: Number; CV: Coefficient of variation; S.D.: Standard Deviation; **%**: Percentage.

the Ife-Ibadan Road (N 07° 22.774` E 04° 01.497`). The occurrence of univalent, as 20 I in AT9 accession on the Ayede-Oye Road (N 07° 50.833` E 05° 20.661`) and 18 II + 4 I in locality Kiwani, AT10 collected on the Itawure-Erinmo Road (N 07° 38.203` E 04° 51.755`) suggests that while these species generally has a chromosome number 2n = 20, there is an isolated instance of the occurrence of 2n = 40 in the Ekiti populations. Accession "Kiwani" featured large biomass typified by a very high number of tillers, broad but short leaves, and dense expression of hairiness and large pollen grains which are typical of polyploidy.

The occurrence of univalent in the AT9 accession on the Ayede-Oye Road (N 07° 50.833` E 05° 20.661`) may be attributed to environmental stress occasioned by the cluster of regrowth forest species that choked the plant. Accession "Kiwani" occurred in an open gravelly ruderal location which had been dug up during road constructions. The plant probably occurred from seed that resulted from the apomictic process.

The cytological evidence from the accessions of *A. gayanus* (2n = 40) studied indicate a regular occurrence of quadrivalent and bivalent associations which suggests that there are four genomes on a basic chromosome number of 10 in *A. gayanus*. The genome can therefore be an allopolyploid (amphidiploid). The configurations 20 II, 2 IV + 16 II and 5 IV + 10 II were recorded in the *A. gayanus* accessions studied.

Okoli (1978) concluded that *A. gayanus* is an allopolyploid based on the karyotypic studies he did. It is significant that Okoli (1978) reported the recovery of a fertile interspecific triploid hybrid between *A. gayanus* and *A. tectorum* in the garden suggesting that such hybrids were through introgression in the wild. No interspecific crosses were formed during the field survey of this study. This does not mean that such hybrids were not occurring; they may be morphologically identical to *A. gayanus* as Okoli (1978) had observed in the artificial triploid hybrids in the garden.

It was observed that the major features of the chromosomes of the accessions studied are regular occurrence of multivalent associations i.e. formation of quadrivalents as chain IV, occurrence of bivalents as ring II and rod II in more frequencies and occasional occurrence of univalents. All the accessions studied conform to the chromosome number of 2n = 40 for *A. gayanus* and 2n = 20 and 2n = 40 for *A. tectorum*. According to Faluyi and Olorode (1987), the occurrence of multivalents and univalent indicate potential for the evolution of aneuploidy and possibilities for change of chromosome number and chromosome repatterning which might lead to genic imbalance and probably viable genetic variability in the species.

The morphological and ecological continuity between *A. gayanus* and *A. tectorum* (Forster, 1962) has led Singh and Godward (1961) to hypothesize that *A.*

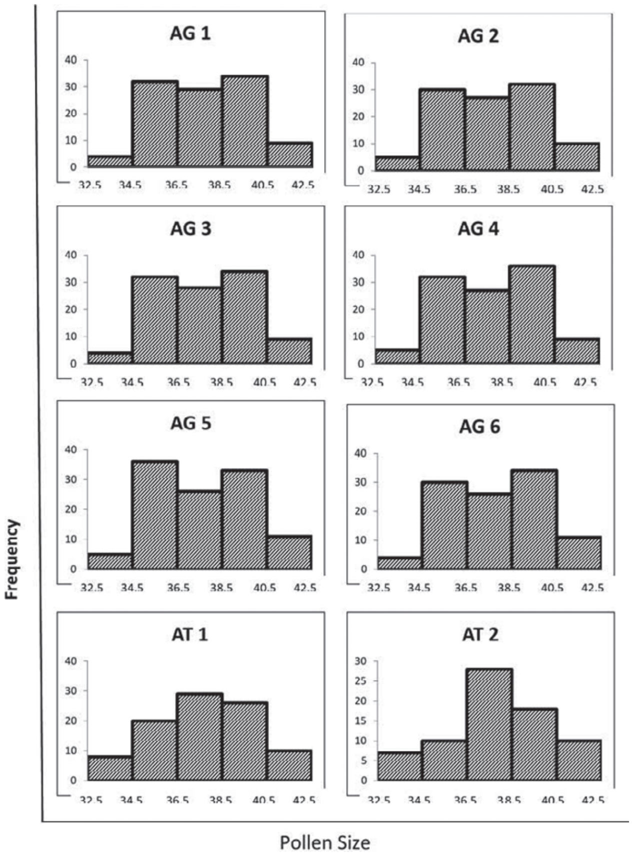

Figure 7. Histogram showing pollen size distribution patterns in the accessions of *Andropogon gayanus-Andropogon tectorum* studied. AG: *Andropogon gayanus*, AT: *Andropogon tectorum*.

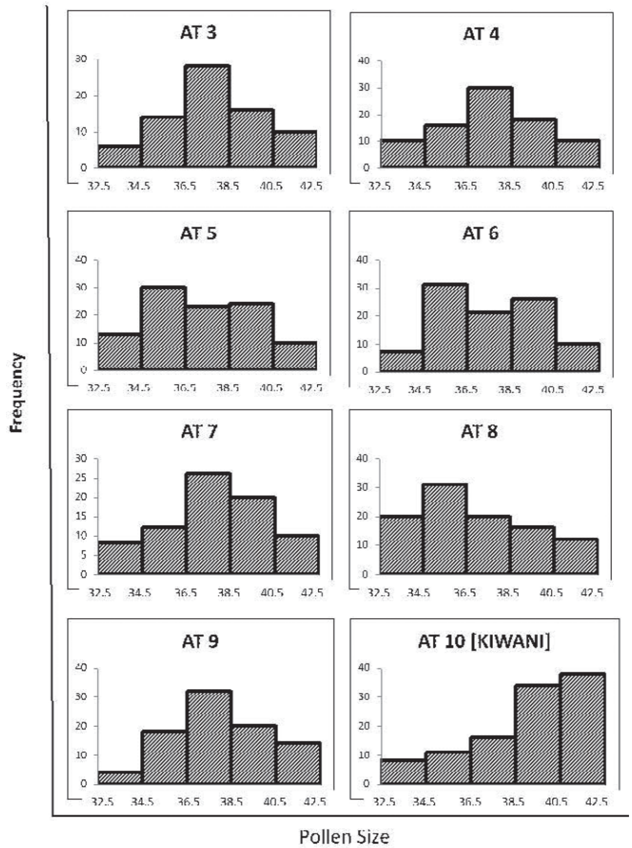

Figure 8. Histogram showing pollen size distribution patterns in the accessions of *Andropogon tectorum* studied. AG: *Andropogon gayanus*, AT: *Andropogon tectorum*.

gayanus (2n =40) resulted from polyploidization of the diploid hybrid between a southern *A. tectorum* and a northern *A. gayanus*. This study pointed to the fact that in *A. tectorum*, the diploid (2n = 20) is ancestral while the higher chromosome numbers are derived. The high incidence of multivalents is suggestive of autoploidy (Stebbins 1950, 1970; Swanson 1968), which means pollen size is high at high ploidy levels. It would be expected that multivalent associations should lead to loss of fertility. The diploid hybrids showed no evidence that the presence of univalent or multivalents were necessarily associated with loss of fertility because all the accessions studied show high pollen viability test and relatively low variability in pollen size. The occurrence of bivalents in the meiotic cells of the species studied suggest that they are allopolyploidy. Also available cytological evidence showed that *A. gayanus* is an allopolyploid while the multivalent associations featuring in diakinesis points to its polyploid (Olorode, 1972).

This study established the occurrence of a tetraploid with a chromosome number of 2n = 40 in one collection of *A. tectorum* from Ekiti State where the chromosome number is predominantly 2n = 20. The details of the cytological studies revealed multiple associations as quadrivalents, bivalents and univalents in the collections of the two species. These events must play major roles in the reproductive and population dynamics of the *Andropogon* complex.

The occurrence of a tetraploid *A. tectorum* is one of the most significant events given the role that this phenomenon and apomixis have been reported to play in the colonization of plants. Hojsgaard (2018) identified the steps involved in the process of polyploidy among which the formation of a triploid arising from a reduced-unreduced gamete fusion is the foundation. This triploid serves as a bridge between parental diploids to produce a derivative tetraploid. The derivative tetraploid produces a new generation of homoploids through a variety of pathways to establish a series of mating partners. The establishment of new polyploids depends on the rate of formation of unreduced (2n) gametes through the apomictic process, frequency-dependent processes that define minority cytotype disadvantages, small effective population sizes and environmental changes that may increase polyploid establishment rates.

Apomixis is the key process that results in the unreduced gamete which is not a product of the regular meiotic process. The unreduced gamete can lead to a polyploid in one step so that apomicts have an advantage in range expansions on account of fitness, vigour and resistance to adverse environmental conditions. Schinkel et al (2016) monitored the correlations of polyploidy and apomixis with elevation and associated environmental gradients in an alpine plant, *Ranunculus kuepferi* using flow cytometry to quantify apomictic and sexual seed formation while seed set and vegetative growth indices were used as fitness parameters. All parameters were correlated to geographical distribution, elevation, temperature and precipitation. Flow Cytometry in their experiment revealed obligate sexuality and facultative apomixis in diploid populations while tetraploid populations were predominantly facultative to obligate apomicts. Apomictic seed formation correlated significantly to higher elevations where niches were at lower temperatures. Diploid apomixis was not successful in range expansion and obligate sexual polyploids were not observed. Facultative apomixis may have aided the colonization of higher elevations but did not necessarily involve long-distance dispersal.

The prospects for the ecological success of the Andropogon complex in its spread down-south looks very bright from the perspectives of its reproductive biology: production of regular seeds by fertilization, haploid and diploid seeds through apomixis; occurrence of plants as facultative or obligate apomicts, production of propagules by rooting at the nodes, preservation of plants as underground rootstocks during the dry season, even in heavily-grazed locations, induction of flushing by fire and the occurrence of tetraploids and aneuploids through natural processes. Apomixis will help the plants to be able to colonize space because it confers self-compatibility as opposed to sexual reproduction where self-incompatibility might be a hindrance according to Baker's Law (Baker 1967)

The incidence of polyploids in the Ekiti populations of *Andropogon tectorum* and their occurrence in restricted gravelly locations sometimes as large populations as on the Ifaki-Ado Road and the occurrence of collections with marked meiotic disturbances also in some Ekiti accessions have been documented. The establishment of the Andropogon complex in the Derived Savanna of the South West is certainly going to involve many polyploids which will get stable as the new habitats and niches get colonized. There will also be intermediate triploids and aneuploids which will arise from the interbreeding between *Andropogon gayanus* and *Andropogon tectorum* some of which will probably be maintained by apomixis and vegetative propagules. This complex will probably be a major part of the vegetation of the Derived Savanna in the near future based on the resilient reproductive strategies that this study and that of Okoli (1978) have revealed.

CONCLUSIONS

The chromosome numbers reported in this study are based on five consistent counts for all accessions. The collections made reflect a substantial endemicity of *A. gayanus-A. tectorum* and accession "Kiwani" is distinct in every regard. From the meiotic studies, a chromosome number of 2n = 20 and 2n = 40 have been established for the species. The occurrence of the tetraploid, chromosome number of 2n = 40 in accession "Kiwani" has been attributed to apomixis occurring in a lonely plant.

AUTHORS' CONTRIBUTIONS

CCN conceived the study. JOF, FMO, CCN realized the experimental work. FMO acquired funding and Data Resources; FMO, CCN did the Writing of review and editing: JOF, supervised. FMO refined the final revision. All authors read and approved the final version of the main manuscript

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