Review Article

Review of the Genus *Andropogon* (Poaceae: Andropogoneae) in America Based on Cytogenetic Studies

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Andropogon is a pantropical grass genus comprising 100–120 species and found mainly in the grasslands of Africa and the Americas. In the new world the genus is represented by approximately sixty (diploids or hexaploids) species grouped in three sections. The hexaploid condition occurs only in the Americas and the full process of this origin is still uncertain, although cytogenetic analysis coupled with taxonomic evidence have provided strong support for new hypothesis. Stebbins proposed the first hypothesis suggesting that the origin of polyploidy in species of *Andropogon* in North America resulted from duplication of the genome of some diploid species, and then by intergeneric crosses with species of a related genus. Since then, numerous studies were performed to clarify the evolutionary history of the genus in America. In this paper, we present a review of cytogenetic studies in the American *Andropogon* species during the last four decades.

1. Introduction

Andropogon L. is a pantropical genus of grasses estimated to contain 100 [1] to 120 [2] species, distributed mainly in the grasslands of Africa and the Americas. *Andropogon* is one of the traditional genera of grasses. Over the course of its circumscription, the genus has included more than 400 species [3] which were subsequently split into several genera [4]. Even considering *Andropogon sensu stricto*, that is, excluding allied genera such as *Bothriochloa* Kuntze, *Dichanthium* Willem., and *Schizachyrium* Nees, the genus remains somewhat heterogeneous [5], especially in the Americas [6, 7]. In the new world the genus is represented by approximately 60 species (see Table 1). The basic chromosome number of the genus is $x = 10$ [6, 8–11], with only a few exceptions [10]. Most African species are diploids or tetraploids ($2n = 2x = 20$; $4x = 40$) [9, 11] and American *Andropogon* species are usually diploid or hexaploid ($2n = 2x = 20$ or $6x = 60$) [2, 6, 7, 12, 13], also with only a few exceptions (see [14]).

Stapf [4] proposed four sections in the genus for African's species: (1) *Andropogon* Stapf, (2) *Leptopogon* Stapf, (3) *Notosolen* Stapf, and (4) *Piestium* Stapf. Gould [6] suggested the incorporation of American species into the first three taxonomic sections mentioned above; these are currently recognized by Clayton and Renvoize [1]. The Americas are exceptionally rich in *Leptopogon* Section members, but poor and with hazy boundaries in the other two sections.

Andropogon has diversified into a larger number of species in America and Africa (see Tables 1 and 2) than in Asia or Europe [1, 11]. Genetic differences between American and African (and within) species are poorly understood. Chromosomal evolution, such as polyploidy, appears to be more extensive in America, as hexaploids are almost entirely restricted to this continent (and especially to South America).

In 1985, based on chromosome counts and morphological issues, Norrmann [7] suggested a difference among species from Argentina that could be applied to other South American species. The number of chromosomes allowed

TABLE 1: Species of *Andropogon* distributed in America.

Taxa	Distribution	2n	Section
A. aequatoriensis Hitchc.	South America	Probably 60	*Leptopogon*
A. arctatus Chapm.	Northern America	20	*Leptopogon* (*A. virginicus* complex)
A. arenarius Hack.	South America	60	*Leptopogon* (*A. lateralis* complex)
A. barretoi Norrmann and Quarin	South America	60	*Notosolen*
A. bicornis L.	Americas	60	*Leptopogon* (*A. lateralis* complex)
A. bourgaei Hack.	Northern America	?	*Leptopogon*
A. brachystachyus Chapm.	Northern America	20	*Leptopogon*
A. brasiliensis A. Zanin and Longhi-Wagner	South America	?	?
A. cabanisii Hack.	Northern America	?	*Leptopogon*
A. campestris Trin.	South America	Probably 60	*Leptopogon*
A. campii Swalen	South America	?	*Leptopogon*
A. canaliglumis Norrmann, Swenson and Caponio	Central America	Probably 60	*Leptopogon*
A. carinatus Nees	South America	Probably 20	*Leptopogon*
A. cordatus Swallen	South America	Probably 60	*Leptopogon*
A. crassus Sohns	South America	Probably 60	*Notosolen*
A. crispifolius Guala and Filgueiras	South America	Probably 60	*Notosolen*
A. cubensis Hack.	Central America	Probably 20	?
A. diuturnus Sohns	South America	Probably 20	*Leptopogon*
A. durifolius Renvoize	South America	Probably 60	*Notosolen*
A. elliotii Chapm.	Northern America	20	*Leptopogon*
A. ekmanii Norrmann, Swenson and Caponio	Central America	Probably 60	*Leptopogon* (*A. lateralis* complex)
A. exaratus Hack.	South America	60, 60+2B	*Notosolen*
A. flavescens J. Presl	South America	Probably 60	*Andropogon*
A. floridanus Scribn.	Northern America	20	*Leptopogon* (*A. virginicus* complex)
A. gerardii Vitman	Northern America	60, 70, 80, 90	*Andropogon*
A. glaucescens Kunth	South America	Probably 60	*Andropogon*
A. glaucophyllus Roseng., B.R. Arrill. and Izag.	South America	60	*Notosolen*
A. glaziovii Hack.	South America	60	*Leptopogon* (*A.lateralis* complex)
A. glomeratus (Walter) Britton, Sterns and Poggenb.	Northern America	20	*Leptopogon* (*A. virginicus* complex)
A. glomeratus var. *glomeratus* (Walter) Britton, Sterns and Poggenb.	Northern America	20	*Leptopogon* (*A. virginicus* complex)
A. glomeratus var. *hirsutior* (Hack.) C. Mohr	Northern America	20	*Leptopogon* (*A. virginicus* complex)
A. glomeratus var. *pumilus* (Vasey) L. H. Dewey	Northern America	20	*Leptopogon* (*A. virginicus* complex)
A. gyrans var. *gyrans* Ashe	Northern America	20	*Leptopogon* (*A. virginicus* complex)
A. gyrans var. *stenophyllus* (Hack.) C. S. Campb.	Northern America	20	*Leptopogon* (*A. virginicus* complex)
A. hallii Hack.	Northern America	60, 70, 100	*Andropogon*
A. herzogii Hack.	South America	Probably 60	*Leptopogon*
A. hondurensis (R.W. Pohl) Wipff	Central America	80	*Andropogon*
A. hypogynus Hack.	South and Central America	60	*Leptopogon* (*A. lateralis* complex)

TABLE 1: Continued.

Taxa	Distribution	2n	Section
A. indetonsus Sohns	South America	Probably 60	Leptopogon
A. lateralis Nees	South and Central America	60, 60+2B	Leptopogon (A. lateralis complex)
A. leucostachyus Kunth	South and Central America	20	Leptopogon
A. liebmannii Hack.	Northern America	20	Leptopogon
A. liebmannii Hack. var. pungensis (Ashe) C. S. Campb.	Northern America	20	Leptopogon
A. lindmanii Hack.	South America	60	Leptopogon (A. lateralis complex)
A. longiberbis Hack.	Northern America	20	Leptopogon (A. virginicus complex)
A. longiramosus Sohns	South America	?	Leptopogon
A. macrothrix Trin.	South America	20	Leptopogon
A. monocladus A. Zanin and Longhi-Wagner	South America	?	?
A. nashianus Hitchc.	Central America	Probably 20	Leptopogon
A. palustris Pilg.	South America	Probably 20	?
A. perdignus Sohns	South America	Probably 60	Andropogon
A. pohlianus Hack.	South America	Probably 60	Notosolen
A. pringlei Scribn. and Merr.	Northern America	?	probably Leptopogon
A. reedii Hitchc. and Ekman	Central America	Probably 20	Leptopogon
A. reinoldii León	Central America	Probably 20	Leptopogon
A. sanlorenzousa Killeen	South America	Probably 20	Leptopogon
A. scabriglumis Swallen	South America	Probably 60	Leptopogon
A. selloanus (Hack.) Hack.	South and Central America	20	Leptopogon
A. sincoranus Renvoize	South America	?	Leptopogon
A. spadiceus Swallen	Northern America	?	?
A. ternarius Michx.	Northern America	40, 60	Leptopogon
A. ternarius var cabanisii (Hack) Fernald and Griscom	Northern America	?	Leptopogon
A. ternatus (Spreng.) Nees	South America	30	Leptopogon
A. tracyi Nash	Northern America	20	Leptopogon (A. virginicus complex)
A. urbanianus Hitchc.	Central America	80	Leptopogon
A. virginicus L.	Northern America	20	Leptopogon (A. virginicus complex)
A. virginicus var. glaucus Hack.	Northern America	20	Leptopogon (A. virginicus complex)
A. virginicus var. virginicus L.	Northern America	20	Leptopogon (A. virginicus complex)
A. vetus Sohns	South America	Probably 60	?

discriminating the genus *Andropogon* into two main groups: a few species are diploid ($2n = 2x = 20$), small in size with colonizing habit; other ten species are hexaploid ($2n = 6x = 60$), larger in size and with varied habitat. South American species consistently display one ploidy level, with hexaploids being considered of alloploid origin [7]. In contrast, there are a few exceptions in North America. For example, two species show intraspecific variation: *Andropogon ternarius* with $2n = 40$ and 60 (which needs reconfirmation) and *Andropogon gerardii* with $2n = 60$ and 90.

To resolve genomic relationships between *Andropogon* species in the new world, many studies were performed until the present. In this paper we present a review of the published results and a general discussion of them.

2. Andropogon Section

In the Americas the *Andropogon* section is well represented by two species *A. gerardii* Vitman and *A. hallii* Hack., distributed mainly in the Northern Hemisphere [14]. The

two species are predominantly hexaploid ($2n = 60$) plants [15–20], however there are populations with high frequency of enneaploids ($2n = 90$) [19, 21–23]. Both species cross in habitat hybridizing zones (e.g., Nebraska sand hills) and hybrid swarms are formed (see [14, 24]). Hybridization in the *A. gerardii-A. hallii* complex was recorded as early as 1891, when an individual was collected in Kansas and described as *A. chrysocomus* Nash [24]. Although hybrids in this combination are fertile, they disappear outside the hybridization habitat, indicating that the species are ecologically distinct [14]. Other members of the section worth mentioning are *A. glaucescens* in South America (no chromosomes count) and *A. hondurensis* (R.W. Pohl) Wipff, with chromosome counts of $2n = 80$.

Stebbins [8] suggested that the polyploid origin of *A. gerardii* in North America could be caused by polyploidization of some diploid of the "Cotton Belt" region, resulting in the constitution of the tetraploid *A. ternarius* (included into the *Leptopogon* section), and then by intergeneric crosses of this tetraploid with species of *Bothriochloa,* which at that time were still regarded as members of *Andropogon,* sect. *Amphilopis. Bothriochloa* includes several species that are adapted to the more arid portions of western North America, and therefore such an origin would be compatible with the more xeric nature of *A. gerardii*. Since at the present time no diploid or tetraploid *Bothriochloa* species exists in North America, Stebbins [8] assumed that the ancestor of these higher polyploids is now extinct.

Norrmann et al. [19] described the meiotic and reproductive behavior in $6x$ and $9x$ cytotypes of *A. gerardii*, and the viability of their hybrids. The meiosis in *A. gerardii* was regular in the hexaploids but irregular in the enneaploids. The hexaploid cytotypes ($2n = 6x = 60$) are fully fertile and produce gametes that uniformly contain 30 chromosomes. Minimal embryo sac abortion and good seed production follow. In the enneaploids, "heptaploids," "octoploids," and aneuploids with $2n = 68 - 78$, gametes frequently abort.

Under controlled pollination, the two common cytotypes can be crossed, producing progeny with a range of chromosome numbers with less fertility [25].

In some natural populations of *A. gerardii* high frequencies of hexaploids and enneaploids, also plants with an intermediate chromosome numbers occur [19, 21, 23]. Populations dominated by or composed of only enneaploids would be much less fertile than mixed populations [19], and indeed such populations are rare to nonexistent [23]. Norrmann and Keeler [25] suggested that the predominance of the hexaploids is related to the higher level of fitness and this could eliminate other cytotypes. In addition the authors suggest that the enneaploids are produced from a hexaploid's unreduced gamete combining with a reduced gamete ($2n = 60 + 30 = 90$).

3. Notosolen Section

Only three South American ($2n = 6x = 60$) species [13] included in this section have yielded chromosome counts: *A. barretoi* Norrmann and Quarin, *A. exaratus* Hack. and *A. glaucophyllus* Roseng., B. R. Arrill. and Izag. The section was considered the most primitive in South America, because of its closeness with species from West Africa [1, 26].

The geographic distribution of these species is relatively restricted and they are not sympatric anymore, even though they live no more than 1000 mi. from each other. However, the hybrid combinations in artificial crossings between the more geographically distant species (*A. exaratus* × *A. glaucophyllus*) are possible and they are fully fertile [11]. Because of the fertility of interspecific hybrids, Norrmann [11] proposed that they have a highly related genomic composition and a probably common origin. The hybrid combinations between *A. barretoi, A. exaratus, A. glaucophyllus* and the trihybrid (*A. exaratus* × *A. glaucophyllus*) × *A. barretoi* are under analysis.

4. Leptopogon Section

Leptopogon is considered the most advanced section within the genus [1, 2, 11] and is characterized by the presence of a concave nerveless first glume of the sessile spikelet [26]. In the Americas, the section is mainly represented by two complexes: *A. virginicus* L., distributed in North America [9] and the *A. lateralis* Ness complex covering South and Central America.

Documented American diploids of this section are represented by twelve species. Nine of them belong to the *A. virginicus* complex (Table 1), and the other three species are distributed in South and Central America: *A. leucostachyus* Kunth, *A. macrothrix* Trin., and *A. selloanus* (Hack.) Hack. Another South American species, *A. ternatus* (Spreng.) Nees. maintains permanent triploidy ($2n = 3x = 30$) by transmitting one genome through the egg cell and two genomes through the sperm nucleus [27]. This species may be best regarded as a diploid with an additional accessory chromosomes set [7, 27].

The hexaploid species are all included in the *A. lateralis* complex and are represented by 10 species restricted to South and Central America, except for *A. bicornis* which has the widest geographical distribution in the group and is also present in North America.

Other uncommon ploidy levels are represented in *A. Notosolen* Michx. ($2n = 40$) and *A. urbanianus* Hitchc. ($2n = 80$).

4.1. Andropogon Virginicus Complex. In North America the *A. virginicus* complex is a closely interrelated group of nine diploid species [9, 28]. These species frequently grow together but rarely produce apparent hybrids [9]. They are effectively reproductively isolated from one another without being separated by large morphological gaps.

Norrmann et al. [29] by genomic in situ hybridization (GISH) studies observed that the South American diploids *A. selloanus* and *A. macrothrix,* and the North American diploid *A. gyrans* Ashe (*A. virginicus* complex member), share the basic *S* genome (Figures 1(a)–1(d)). This was previously proposed based on classical hybridization and meiotic chromosome behavior studies by Galdeano and Norrmann [12] for the first two species and reveals that the S

TABLE 2: Species of *Andropogon* distributed in Africa.

| Taxa	Distribution	2n	Section
A. abyssinicus R. Br. ex Fresen.	East Africa	32	*Andropogon*
A. africanus Franch.	Africa	40	*Leptopogon*
A. amethystinus Steud.	Africa	20, c.30	*Andropogon*
A. amplectens Nees	Southern Africa	40	*Piestium*
A. appendiculatus Nees	Southern Africa	20, 40, 60	*Notosolen*
A. ascinodis C.B. Clarke	Africa and India	40	probably *Notosolen*
A. auriculatus Stapf	West Africa	?	?
A. brachyatherus Hochst.	Southern Africa	20	?
A. brazzae Franch.	Southern Africa	20, 40	?
A. canaliculatus Schumach.	Africa	20	*Piestium*
A. chevalieri Reznik	West Africa	?	?
A. chinensis (Nees) Merrill	Africa and Asia	?	*Piestium*
A. chrysostachyus Steud.	East Africa	?	?
A. curvifolius Clayton	West Africa	20	*Leptopogon*
A. distachyos L.	Africa/Europe	36, 40	*Andropogon*
A. dummeri Stapf	West Africa	20	?
A. eucomus Nees	Africa	20, 40	?
A. filifolius (Nees) Steud	Southern Africa	?	*Piestium*
A. gabonensis Stapf	West Africa	20, 21	?
A. gayanus Kunth	Africa and Asia	20, 35, 40, 42, 43, 44	*Notosolen*
A. gayanus Kunth var *bisquamulatus* (Hochst.) Hack.	Africa and Asia	40	*Notosolen*
A. gayanus Kunth var *gayanus*	Africa and Asia	40	*Notosolen*
A. gayanus Kunth var *squamulatus* (Hochst) Stapf.	Africa and Asia	40	*Notosolen*
A. guianensis Kunth ex Steud.	Africa	40	?
A. heterantherus Stapf	East Africa	?	*Piestium*
A. huillensis Rendle	Southern Africa	20, 60, 100	*Leptopogon*
A. ivorensis Adjan. and Clayton	West Africa	40	?
A. kilimandscharicus Pilger	Africa	20	*Andropogon*
A. laxatus Stapf	Africa	?	*Leptopogon*
A. lima (Hack.) Stapf	Africa	?	*Andropogon*
A. macrophyllus Stapf	West Africa	40	?
A. mannii Hook. f.	Africa	14	*Andropogon*
A. patris Robyns	Africa	20	?
A. perligulatus Stapf	Africa	20	?
A. pinguipes Stapf	West Africa	?	?
A. pratensis Hochst.	West Africa	?	*Andropogon*
A. pseudapricus Stapf	Africa	20, 40	*Piestium*
A. pusillus Hook. f.	West Africa	?	?
A. schinzii Hack.	Africa	20, 40	*Piestium*
A. schirensis Hochst. ex A. Rich.	Africa	20, 40	*Piestium*
A. tectorum Schumach. and Thonn.	West Africa	20, 23, 30, 40	*Notosolen*
A. textilis Rendle	East Africa	?	*Piestium*

(a)

(b)

(c)

(d)

(e)

(f)

(g)

(h)
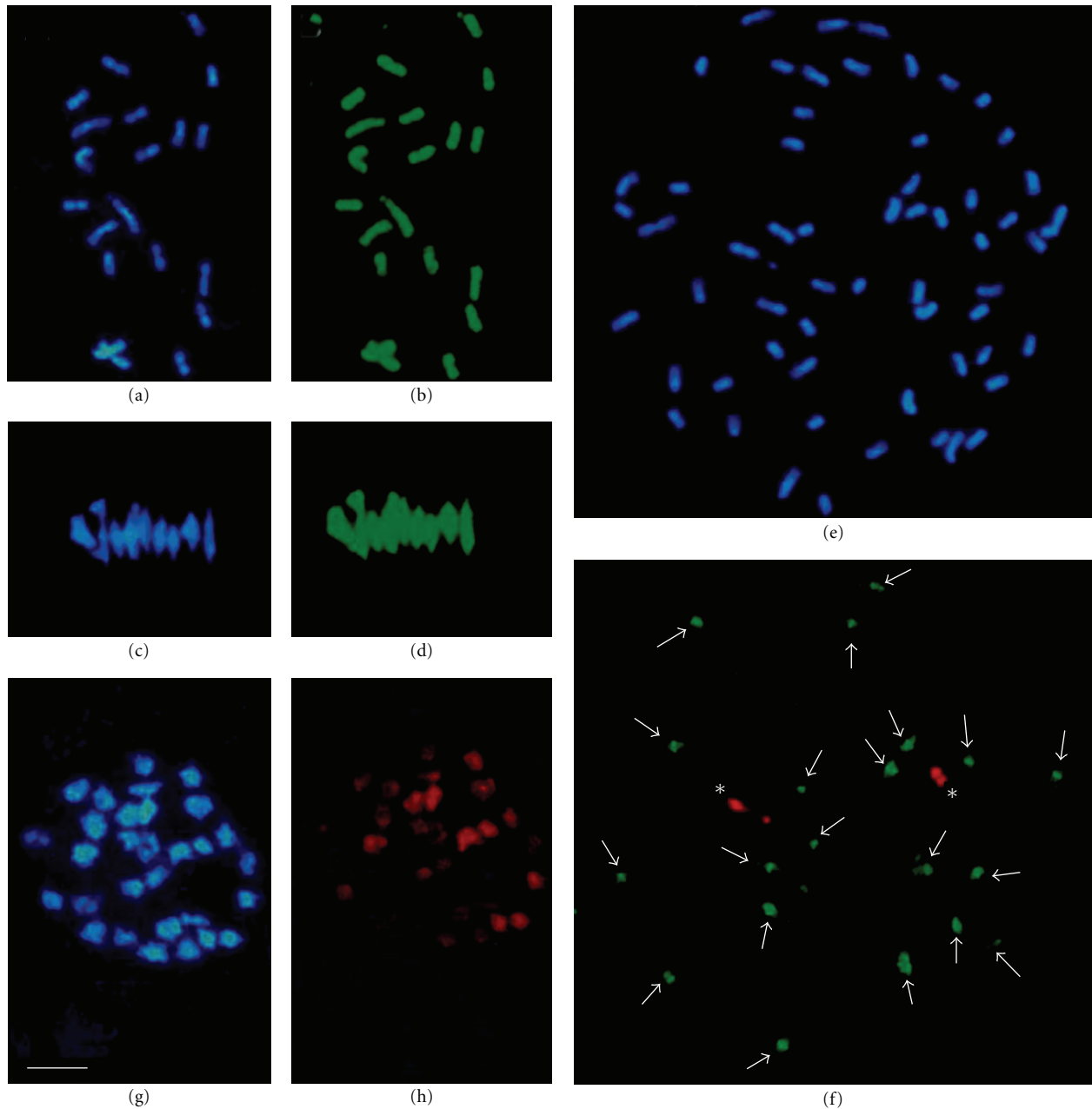
FIGURE 1: GISH on mitotic and meiotic metaphase chromosomes of (a–d) diploid ($2n = 2x = 20$) and (e–h) hexaploid ($2n = 6x = 60$) *Andropogon* species. (a) and (b) Mitotic chromosomes of SA diploid *A. selloanus* probed with genomic DNA from SA diploid *A. macrothrix* and detected with green fluorescence. (a) DAPI-stained chromosomes; (b) GISH showing all 20 chromosomes fluorescing green. (c) and (d) Meiotic chromosomes of SA diploid *A. selloanus* probed with genomic DNA from the NA diploid *A. gyrans* and detected with green fluorescence. (c) DAPI-stained chromosomes; (d) GISH showing all 10 bivalents fluorescing green. (e) and (f) Mitotic chromosomes of SA hexaploid *A. lateralis* probed simultaneously with genomic DNA from the SA diploid *A. selloanus* (green fluorescence) and pTa71 (red fluorescence). (e) DAPI-stained chromosomes; (f) GISH showing 20 chromosomes fluorescing green (*S* genome chromosomes, arrows) and two sites of red hybridization (asterisks) corresponding to the location of the 18S.25S rDNA on two chromosomes that do not fluoresce green and thus do not originate from the S genome. (g) and (h) Meiotic chromosomes of SA hexaploid *A. lateralis* probed with genomic DNA from the NA diploid *A. gyrans* and detected with red fluorescence. (g) DAPI-stained chromosomes; (h) GISH showing approximately 10 bivalents fluorescing red. Scale bar = 2 μm. Figure extracted from [29].

genome, originally defined for the South American diploids, is also shared by the North American diploid *A. gyrans*. Since *A. gyrans* is a member of the *Andropogon virginicus* group, whose monophyly was demonstrated by classical taxonomy [9], it is likely that the remaining members of the *A. virginicus* group also contain the S genome [29].

4.2. Andropogon lateralis Complex. This section is geographically distributed in South and Central America and is constituted entirely by hexaploid species: *A. arenarius* Hack., *A. bicornis* L., *A. glaziovii* Hack., *A. hypogynus* Hack., *A. lateralis* Nees, *A. × subtilior* (Hack.) Norrmann (pro. spp.), *A. × lindmanii* Hack. (pro. spp.), and *A. × coloratus* Hack. (pro. spp.), among others, which present the anther size and the number of pollen grains in fertile sessile spikelets strongly reduced compared with those of pedicellate spikelets. This synapomorphy of dimorphic anthers defines this complex [2, 9]. Within this complex, natural interspecific hybrids have been reported, where populations of different species live in sympatry. Three combinations were reported by Campbell and Windish [2] and two more by Norrmann [11]. Of the ten taxa that comprise the complex in the southern area of South America, five are legitimate species and the others are interspecific hybrids [30].

Norrmann et al. [29] performed GISH studies on two hexaploid species of the *A. lateralis* complex: *A. lateralis* and *A. bicornis*. Hybridization of genomic DNA from the South American diploid *A. selloanus* onto mitotic chromosomes of the South American hexaploid *A. lateralis* resulted in only 20 out of the 60 chromosomes showing strong green fluorescence (Figures 1(e) and 1(f)). These results indicate that *A. lateralis* is an allohexaploid in which the S genome comprises only one of the other genomes. Interestingly, however, the 20 S genome chromosomes were not uniformly labeled along their entire length (as in the diploids, see Figures 1(a)–1(d)); instead, the labeling was mainly concentrated in the pericentromeric regions. These results suggest that there has been some divergence of the repetitive sequences in the distal regions of the S genome chromosomes since the allopolyploid was formed so that they no longer hybridize to the S genome probe.

When meiotic chromosomes of *A. lateralis* were probed with genomic DNA from the North American diploid *A. gyrans*, the overall results were similar to those using the South American diploid *A. selloanus* as a probe, although slight differences in labeling intensity were sometimes observed, suggesting once again that there has been some divergence of the repetitive DNA sequences between the S genome in the North American diploid and hexaploid species as suggested above for *A. lateralis* (Figures 1(g)–1(h)).

Norrmann [30] analyzed the chromosomes and meiotic behavior between interspecific hybrids into the *A. lateralis* complex and observed that all studied hybrids showed $2n = 60$ chromosomes which pair to form up to 30 bivalents per pollen mother cell. The high frequency of bivalents observed in all crosses (30 observed, of 30 maximum) points to the existence of ancient chromosomal homology or homoeology in all species treated, with small differences among the "three" basic genomes (see [29]).

5. Intersectional Analysis

Norrmann [11] crossed *A. barretoi* (*Notosolen*) with *A. gerardii* (section *Andropogon*) and observed a high chromosome pairing in these hybrids. But this pairing does not result from true homology, according to genomic in situ (GISH) experiments carried out recently (Norrmann and Leitch, unpubl. data), which evidence very low homologies among chromosomes from each parental species. The formation of multivalent as a divergence phenomenon is strongly suggested by the odd meiosis, with irregular segregation and formation of multiple nuclei.

Intersectional hybrids among *A. lateralis* (*Leptopogon*) and *A. exaratus* (*Notosolen*) occur in nature and can be experimentally produced [11]. GISH experiments carried on this hybrid revealed very low homologies among these species (Norrmann and Leitch, in prep). On the other hand, upon direct labeling of *A. gerardii* (*Andropogon*) onto *A. bicornis* (*Leptopogon*), much more homologies appear (Norrmann and Leitch, in prep). All these results suggest section *Notosolen* has no close relationships to *Andropogon* or to *Leptopogon* sections.

Finally, preliminary results on *A. gerardii* chromosomes hybridizing to probes from *A. gyrans* suggest a genomic formula SS S^1S^1XX for *A. gerardii* with one genome close to *A. gyrans* (S), another less related (S^1), and a third unrelated (X) (Nagahama and Norrmann, unpubl. data).

6. Discussion

To resolve genomic relationships between *Andropogon* species, previous studies have successfully made interspecific hybrids among diploids [12], among diploids and triploids [27], among hexaploids [11, 19, 30, 31], between hexaploids with enneaploids and inner aneuploids [19, 25] and among diploid and hexaploid species [29]. While the later study suggests that the diploid South American species *A. selloanus* and *A. macrothrix* and the North American diploid *A. gyrans* share a common genome, relationships between the North and South American species are still unclear. This was due in part to the failure to make diploid × hexaploid crosses in several combinations [12].

Stebbins [8] suggested that the North American hexaploids (*A. gerardii*) probably were originated in the new world through processes of polyploidization of diploid species of *Andropogon*, followed by hybridization with species of *Bothriochloa*. Several events have happened since then. First, this hypothesis was proposed by the time hexaploids in South America were not known, as the first chromosome counts were published between 1985 [7] and 1986 [2]. Second, GISH experiences suggest that *Bothriochloa* and *Andropogon* have stronger chromosomal divergences than thought before (Norrmann, unpubl. data). Finally, the similarity suggested by Stebbins [8] among species of the genera *Andropogon* and *Bothriochloa* actually are recognized as evolutionary convergence [1]. Moreover, Stebbins' hypothesis suggests that *A. gerardii* and other polyploid complexes were distributed on the plains of central North America about 5 million years ago. However, due to

the last glaciations, it is known that the colonization of the North American prairies by this species was recent, and this happened not earlier than 10,000 years ago. Nowadays, there is consensus in the origin of *A. gerardii* in Central America or Northern South America, and after the retreat of the ice, it would have colonized the North American plains. This hypothesis is also supported by the octoploid *A. hondurensis*, distributed in Central America, due to that this species is related with *A. gerardii*, being considered in the past as subspecies of *A. gerardii* (see [32]).

Stebbins' hypothesis has two parts: first, the conformation of a tetraploid from diploids of the cotton belt and second, the hybridization with *Bothriochloa* species. As we have explained before, second part needs modification but part 1, that is, the generation of hexaploids as an American evolutionary process stands still as the more solid hypothesis, at least for *A. gerardii* and the *A. lateralis* complex, and would also have occurred in genera related to *Andropogon*, for example in *Bothriochloa* [8, 33, 34]. This hypothesis is sustained by GISH experiments pointing to the S genome as being part of *A. gerardii* and the *A. lateralis* genome. Different forms of the S genome are present in American diploid species, as *A. selloanus* or the *A. virginicus* complex and none of these species lives in Africa. Therefore, the origin of *A. gerardii* and the *A. lateralis* complexes could be American, with the providers of the other/s genomes still not found.

On the other hand, it is worth mentioning other hypothesis for the origin of the hexaploids. Norrmann [11] suggested that one or more ancestral hexaploids might have been established both in America and Africa at least in the Cretaceous (60 million years ago). The lack of hexaploid species in Africa could be due to these polyploids proliferating adaptively in America, and not in Africa due to selective pressure, because the continent underwent dramatic changes and rigorous conditions after the separation from the Americas [35, 36]. Another possibility is that the hexaploids do exist, but they have not been found. There are records of an African hexaploid (*A. huillensis* Rendle) [37], but in this species also are recorded chromosome counts with $2n = 20$ [38] and $2n = 100$ [39], suggesting that this polyploidization was because of genome duplication (autopolyploid), and not as in the American hexaploids which are allopolyploids.

Our view of the *Andropogons* in America is much complete nowadays than it was in 1975. Great advances have been made in major issues, as the understanding of the *A. virginicus*, the *A. lateralis*, and the *A. gerardii-A.hallii* complexes and their cytogenetics.

GISH technique has proved useful and overcomes the difficulty in making $2x$–$6x$ hybrids and studying intersectional hybrids. Also, preliminary results based on molecular marker analysis suggest that in the *A. lateralis* complex there are at least two clearly different genomes. On the other hand, the three genomes of sect. *Notosolen* appear to be related (Nagahama and Norrmann, unpubl. data).

We need to be cautious about the comprehension of the whole genus since we are still based on chromosome counts made for only a portion of the species. No cytogenetic information is available from northern Brazilian species, or

from Venezuela, Colombia, Equator, Peru (*A. glaucescens* and *A. flavescens* from the *Andropogon* section) and other species from Central America and West Indies. If diploids could be differentiated from hexaploids by its size, as Norrmann proposed [7], then many South and Central American species could be candidates to look for other genome sources different from S (see Table 1).

Finally, old grasslands hexaploid species as *A. gerardii* and members of the *A. lateralis* complex are under the anthropogenic pressure. The days of the North American plains covered with *A. gerardii* feeding bison, or Venezuelan "llanos" and "campos" of southern South America (NE Argentina, S Brazil, Paraguay, Uruguay) dominated by *A. lateralis* and *A. hypogynus* are not the actual picture, but the species are still there. Concern should perhaps be put on the few American members of the *Notosolen* section: *A. exaratus* survives well because it lives on the marshes, but *A. glaucophyllus* (in dunes of southern Brazil and Uruguay) is loosing presence. The worse situation we are aware is that of *A. barretoi*, which can only be found alongside the road Santa María to Porto Alegre, as related to one of us by Professor Ismar Barreto, the real discoverer of the species back in 1982. Today, the habitat stretches no more than 10 mi. along the roadside.

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