

中国西南六种广义拂子茅属 (禾本科) 植物的染色体数目*

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摘要: 广义拂子茅属 (*Calamagrostis*) 是一个世界温带广布的大属, 有些作者又分为拂子茅属和野青茅属, 但近期的研究表明处理为一个属较为合适。中国共有 37 种广义拂子茅属植物, 但至今没有任何染色体的研究。本文报道了其中产于中国西南 6 种野青茅的染色体数目, 其中 *Deyeuxia petelotii* 4 个居群, *D. diffusa*, *D. moupinensis*, *D. nivicola* 和 *D. flavens* 各一个居群都是四倍体 ($2n=4x=28$), *D. neglecta* 为六倍体 ($2n=6x=42$)。根据广义拂子茅属植物染色体倍性特征, 该属植物中至今未发现二倍体, 四倍体是该属中倍性最低和最普遍的, 广义拂子茅属的演化很可能是在四倍体的水平上进行的。由于以上几个四倍体种均是狭域分布的类群, 所以可能是由四倍体的祖先隔离分化形成的。

关键词: 野青茅属; 拂子茅属; 染色体数目; 四倍体; 六倍体

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Chromosome counts in the Genus *Calamagrostis* s. l. (Poaceae) from Southwestern China*

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Abstract: *Calamagrostis* s. l. is a large genus widespread throughout the world in temperate and cold regions. It is sometimes divided into two genera: *Calamagrostis* s. str. and *Deyeuxia*, and both have been accepted in China, while recent studies show it should be treated as one genus. There are 37 species of *Calamagrostis* s. l. occurring in China, but no cytological study was conducted before. In this paper the chromosome numbers of 9 populations representing 6 species of *Deyeuxia* (recognized as a part of *Calamagrostis* s. l.) from southwestern China are reported for the first time. Most of them are tetraploids and no diploid species is found. All 4 populations of *D. petelotii* and each population of *D. diffusa*, *D. moupinensis*, *D. nivicola*, and *D. flavens* are tetraploids ($2n=4x=28$), and the only population of *D. neglecta* is hexaploid ($2n=6x=42$). On the basis of these counts and previous reports, tetraploid is again confirmed primitive in *Calamagrostis* s. l. and the speciation of the genus is principally occurred at tetraploid level in this region. As these five tetraploid species are restricted to Himalayan-Hengduan Mountains, they probably have been formed by isolation from tetraploid ancestors.

Key words: *Deyeuxia*; *Calamagrostis*; Chromosome number; Tetraploid; Hexaploid

Calamagrostis Adans. s. l. belongs to the tribe Aveneae, subfamily Pooideae of Poaceae, and it contains about 270 species (Clayton and Renvoize, 1986). The genus is widespread throughout the world in temperate and cold regions and on tropical mountains (Clayton and

Renvoize, 1986). Central Asia, eastern Australia, and the Andes Mountains of South America are three distribution centers of the group (Tateoka, 1974).

Calamagrostis s. l. has been divided on the basis of morphological features into sections (Koch, 1837; Torg

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es, 1898; Rozhevitz, 1934; Tsvelev, 1983) or subgenera (Wasiljew, 1960). Some authors, following the generic delimitation of Beauvois (1812), treat it as two genera: *Calamagrostis* s. str. and *Deyeuxia* (Rúgolo, 1978; Edgar, 1995; Renvoize, 1998). In fact, *Deyeuxia* makes up the majority of *Calamagrostis* s.l. with over 250 out of total 270 species in *Calamagrostis* s.l. (Clayton and Renvoize, 1986), and so for *Deyeuxia* species, *Deyeuxia* and *Calamagrostis* are two interchangeable names. For Chinese species, Keng (1959), Lu (1987) and Chen (2001) all recognized two genera, only Yang (1983, 1988) recognized *Calamagrostis* s.l.. As all previous cytological studies outside China were carried out on the basis recognizing *Calamagrostis* s.l., and the split of two genera is not supported by our molecular phylogenetic study (Ma *et al.*, unpubl. data), it must be addressed that the species in the present study, though using the generic name *Deyeuxia* as conventionally did in China, are regarded as species of *Calamagrostis* s.l. (this will be abbreviated as *Calamagrostis* in the following parts).

52 species of *Calamagrostis* have previously been studied cytologically in the world. Chromosome numbers of *Calamagrostis* have been recorded from Europe (e.g. Löve and Löve, 1961, 1974; Fedorov, 1969; Arohonka, 1982; Micieta, 1986; Petrova and Stoyanova, 1998; Lökvist and Hultgård, 1999), the far east of Russia (Zhukova, 1967, 1969; Zhukova and Tikhonova, 1971, 1973; Zhukova and Petrovsky, 1971, 1975; Guzik, 1984; Rudyka, 1988, 1990; Sorokin, 1991, 1993; Probatova *et al.*, 1996), Kashmir (Koul and Gohil, 1991), Himalayas (Mehra and Sharma, 1975), Japan (Tateoka, 1976, 1978, 1984), North America (Greene, 1984; Aiken *et al.*, 1989), and Costa Rica (Pohl and Davidse, 1971). Overall, the genus has been studied in Northern Hemisphere except China but not studied in Southern Hemisphere. Pre-

vious studies show that species in *Calamagrostis* have large Pooid type chromosomes, which is characteristic for Pooid grasses and unique in Poaceae (Clayton and Renvoize, 1986), and the chromosome base number is 7. Various levels of ploidy have been found in the genus: tetraploid, hexaploid, octoploid, decaploid, dodecaploid, and aneuploid, and different polyploidy in one species is common in the genus (Tateoka, 1976). No diploid has been found in any of the previous studies, and some specialists (Nygren, 1962; Tateoka, 1976) proposed that the tetraploid is primitive in the genus.

There are 37 species of *Calamagrostis* in China, including 6 species of *Calamagrostis* s. str. (Lu, 1987) and 31 species of *Deyeuxia* (Chen, 2001), and especially rich in southwestern China (abbreviated as SW China below) along Himalaya-Hengduan Mountains. No cytological work on the species from China has been conducted before. The present work is to investigate chromosome numbers of some species in SW China so as to provide data for further systematic work for the genus.

Material and Methods

Seeds or living plants were collected from field for further experiment in various localities in SW China. Plants from one population were studied for each species, but four populations were studied for *Deyeuxia petelotii* because it used to have a controversial systematic position. About 3–10 individuals were used for each population. The localities and the herbarium voucher specimens are listed in Table 1. Herbarium voucher specimens are deposited in KUN (Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China).

Root tips were used for chromosome count. Root tips were mostly obtained from germinating seeds, and only in two populations of *Deyeuxia petelotii*, one in Kunming (H. Y. Ma 001) and one in Bijie (H. Y. Ma 154), the root tips were obtained from the transplanted plants.

Table 1 Material of *Calamagrostis* s.l. studied and chromosome numbers determined, localities and voucher specimens

Species	2n	Locality	Voucher
<i>Deyeuxia petelotii</i> (Hitchcock) S. M. Phillips & W. L. Chen	28	Heilongtan, Kunming, Yunnan, 1900 m	H. Y. Ma 001
	28	Lidiping, Weiki County, Yunnan, 3000 m	H. Y. Ma 008
	28	Mt. Cangshan, Dali, Yunnan, 3000 m	H. Y. Ma 144
	28	Yang Hill, Bijie County, Guizhou, 1450 m	H. Y. Ma 154
<i>D. flava</i> Keng	28	Mt. Haba, Shangri-la County, Yunnan, 2700 m	H. Y. Ma 119
<i>D. diffusa</i> Keng	28	Xiaoshao, Kunming, Yunnan, 2000 m	H. Y. Ma 159
<i>D. nivicola</i> Hook. f	28	Xiangcheng County, Sichuan, 4300 m	H. Y. Ma 63
<i>D. moupinensis</i> (Franch.) Pilger	28	Ganyanggou, Baoxing County, Sichuan, 2600 m	H. Y. Ma 256
<i>D. neglecta</i> (Ehrl.) Kunth	42	Mt. Zhegu, Maerkang County, Sichuan, 4300 m	H. Y. Ma 240

The root tips were pretreated in a mixture of 0.002 mmol/L 8-hydroxyquinoline and saturated 1, 4-dichlorobenzene (1:1 in volume) for 5–6 hours at room temperature, then fixed with Carnoy's fluid at 4°C for at least one hour. Before staining, the root tips were hydrolysed with 1 mmol/L HCl for 15 min at 60°C. Finally, samples were stained with carbofuchsin and squashed. From each population at least ten cells were counted. Photographs were taken with Olympus BX 51.

Results

D. petelotii (Hitchcock) S.M. Phillips & W.L. Chen

The species is special in *Calamagrostis* because its glumes are usually slightly shorter than the lemma, while most species in *Calamagrostis* have glumes longer than or equal to the lemma. For this unique feature, the species has been described as new several times in different genera: *Aulacolepis petelotii* Hitchcock, *Agrostis continentalis* Handel-Mazzetti, and *Anisachne gracilis* Keng, and

several combinations have been made: *Aniselytron gracilis* (Keng) N. X. Zhao, *A. petelotii* (Hitchcock) Soják, *Calamagrostis petelotii* (Hitchcock) Govaerts, *Deyauxia continentalis* (Handel-Mazzetti) L. Liou, and *Neaulacolepis petelotii* (Hitchcock) Rauschert (Phillips and Chen, 2003). The latest revision identifies it as *Deyauxia petelotii* (Hitchcock) S. M. Phillips & W. L. Chen (Phillips and Chen, 2003).

This species appears quite widespread from north-eastern India through southern China to northern Vietnam, at elevations of 1000–3400 m (Phillips and Chen, 2003). In China, it is distributed in Guizhou and Yunnan and grows at grassy places on sandy acid soils at altitudes of 1400–2000 m (Chen, 2001). Our result shows that the species is a stable tetraploid in China since all four populations from Yunnan and Guizhou have chromosome number 28 ($2n=4x=28$) (Fig. 1: 1).

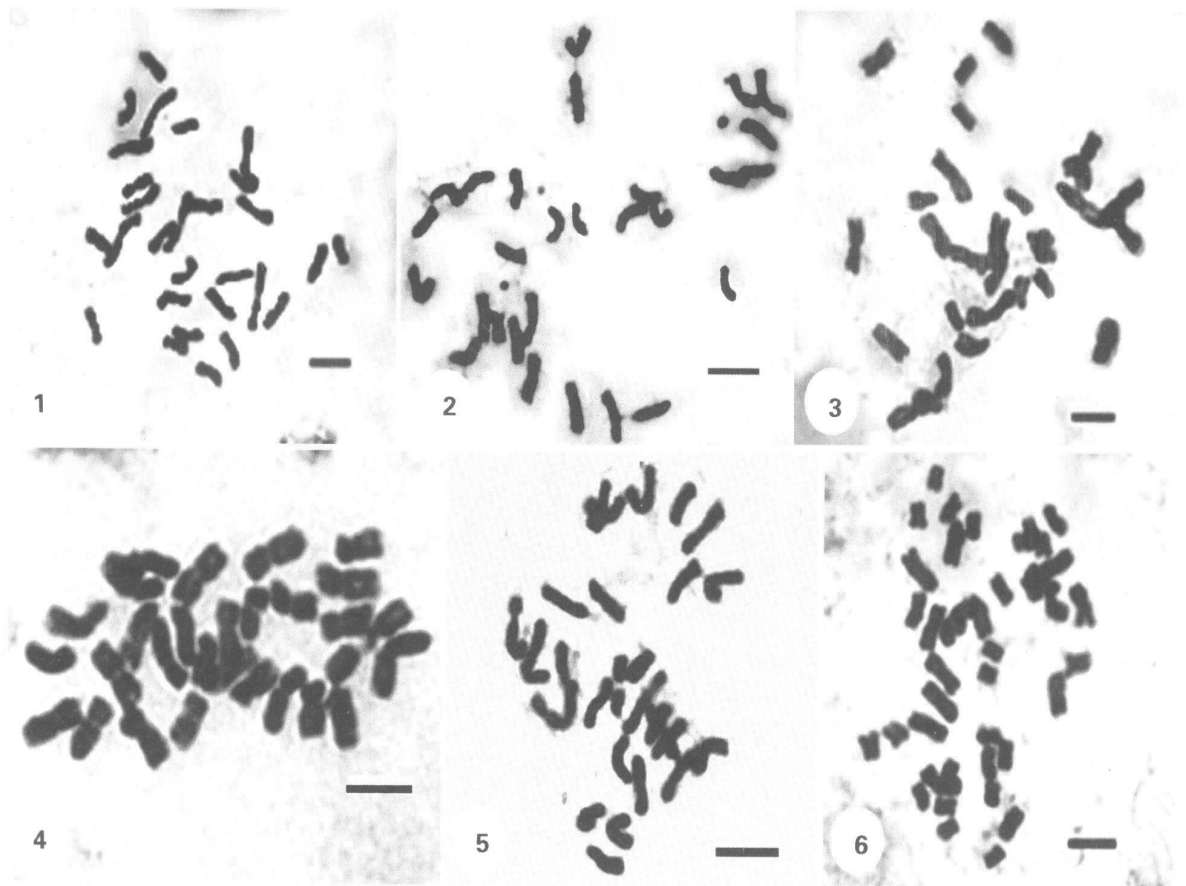


Fig. 1 Mitotic metaphases in species of *Deyauxia*

1. *Deyauxia petelotii* ($2n=28$); 2. *D. nivicola* ($2n=28$); 3. *D. flava* ($2n=28$); 4. *D. diffusa* ($2n=28$);
5. *D. moupinensis* ($2n=28$); 6. *D. neglecta* ($2n=42$) Scale bar= 5 μ m

***D. nivicola* Hook. f**

The species is distributed in Qinghai, Sichuan, Xizang, and Yunnan of China, as well as Nepal and Sikkim (Chen, 2001). It grows on grassy and stony mountain slopes at altitudes of 3000–5000 m. We collected seeds from Xiangcheng County, Sichuan Province, and it is a tetraploid ($2n=4x=28$) (Fig. 1: 2).

***D. flavens* Keng**

The species is distributed relatively wide in Qinghai-Tibet Plateau, Gansu, Qinghai, Sichuan, Xizang and Yunnan (Chen, 2001). It grows in alpine meadows, grassy slopes, open woodland or shrubland, especially along riverbanks, at altitudes of 2800–4500 m. We collected seeds from Mt. Haba in Shangrila County, Yunnan, and it is determined a tetraploid ($2n=4x=28$) (Fig. 1: 3).

***D. diffusa* Keng**

It is restricted to Guizhou, Sichuan, and Yunnan Provinces of China and grows among shrubs and on wasteland at altitudes of 1900–3800 m (Chen, 2001). The seeds were collected from Kunming, Yunnan and it is a tetraploid ($2n=4x=28$) (Fig. 1: 4).

***D. moupinensis* (Franch.) Pilger**

The species is restricted to a few counties in Sichuan, and grows in very moist grassy places in montane forests at altitudes of 2000–2600 m (Chen, 2001). We collected seeds from the locality of its holotype specimen, Baoxing County in Sichuan Province. It is a tetraploid ($2n=4x=28$) (Fig. 1: 5).

***D. neglecta* (Ehrh.) Kunth**

This is a widespread, highly polymorphic species, growing at grassy places in forests and damp ground near ditches at altitudes of 1200–4000 m. In China, it is distributed in Gansu, Hebei, Heilongjiang, Liaoning, Inner Mongolia, Shanxi, Sichuan, and Xinjiang (Chen, 2001). It is also distributed in Japan, Kyrgyzstan, Russia, Mongolia, Tajikistan, Europe and North America. We collected seeds from one population in Sichuan Province and it is a hexaploid ($2n=6x=42$) (Fig. 1: 6).

Discussion

This is the first report of chromosome numbers of *Calamagrostis* in China. In accord with the previous

studies on *Calamagrostis*, species in our study all have large size chromosomes and have a stable basic number 7, which are called “Festucoid” (Stebbins, 1956) or “Poooid” (Clayton and Renvoize, 1986) type chromosomes and characteristic in Poooid grasses.

Including the present study, altogether 57 species of *Calamagrostis* have been studied cytologically. Early researchers (Nygren, 1962; Tateoka, 1976) had found that diploid plants with $2n=14$, as well as triploids and pentaploids, are complete lacking while tetraploids are dominant in *Calamagrostis*. Meanwhile, studies on reproduction of *Calamagrostis* showed that tetraploid plants ($2n=28$) are sexual while hexaploids ($2n=42$) are apomictic, indicating that tetraploid plants behave like a diploid plant while hexaploid plants like a triploid (Nygren, 1962).

Stebbins (1956) pointed out that polyploid complex may pass through a series of stages. In polyploid complexes in which no diploid species is found, the present-day polyploids could not have formed from diploids, for if that, diploids, at least some relics, should still be found as narrow endemics. In this kind old polyploid complex, nearly all of the diploid species have become extinct, and new cycles of polyploidy have arisen, and tetraploids has become actual diploids (Stebbins, 1956). Based the reproductive mode of *Calamagrostis*, Nygren (1962) thus regarded tetraploid as primitive in the genus. Based on intensive study of chromosome numbers of Japanese species, in combination with data from Europe, Tateoka (1976) assumed that a tendency towards the basic number of $X=14$ have been developed in earlier stage and present-day Japanese species have been formed from tetraploid ancestral taxa, and further he postulated that this should also be applicable to Europe species.

After these studies, many new chromosome counts for species in Northern Hemisphere have been reported in 1980s and 1990s, but still no diploid plant with $2n=14$ was found, all species have chromosome numbers above 28. The lacking of diploid in *Calamagrostis* is still questionable since that no species in tropics and Southern Hemisphere has been studied, but the chance to find diploid plant in those areas is very small. In genera related to *Calamagrostis*, such as *Agrostis*, which has very sim-

ilar distribution pattern as *Calamagrostis* does, diploid plants with $2n = 14$ are not scarce, but all from Northern Hemisphere, none of species in Southern Hemisphere is found diploid (Frey, 1997).

Greene (1984) studied reproduction of some eastern North American species. Tetraploids and polyploids are found again in that region. His work also confirmed that tetraploids are sexual, while hexaploids ($2n = 42$) are apomictic in seed formation. Moreover, tetraploids always have distinct morphology easy to distinguish from other species whereas hexaploids are not distinct in morphology and often show somewhat intermediate characters. This again confirmed that tetraploids actually behave like a diploid while hexaploids behave like a triploid, thus agreeing to Tateoka's (1976) postulation that the evolution of the genus occurred at tetraploid level.

In our investigation on Chinese species, in accord with other parts of the Northern Hemisphere, no diploid is found. Of the 6 species in our study, 5 are tetraploids, and only one species *D. neglecta* is a hexaploid. Therefore all previous studies and our current study confirmed again that tetraploid is dominant in the genus, and then it is reasonable to suggest that the speciation of *Calamagrostis* in China has occurred at the tetraploid level.

Then it is possible to consider the speciation mode of these species from their chromosome numbers and distribution patterns. All 5 tetraploid species are restricted to Qinghai-Tibet Plateau or Himalayan-Hengduan regions, so they probably have been formed by isolation from widespread tetraploid ancestors during the uplift of the Himalayas. As no ploidy level above tetraploid has been found, it seems that no polyploidization has involved during the process of speciation. This is in accord with the recent summary on chromosomal studies on plants in Hengduan mountains (Nie *et al.*, 2005), which shows that the polyploidy is not as common as people have assumed and the speciation in the region have principally occurred at diploid level, only to note that the tetraploids in *Calamagrostis* are in fact diploids.

Among these 5 species, *D. petdotii* used to have controversial systematic position. It has now been widely recognized as a species of *Calamagrostis* (Clayton and Renvoize, 1986; Chen, 2001; Phillips and Chen,

2003), and our recent molecular study also show that it is a member of *Calamagrostis* (Ma *et al.*, unpubl. data). In this study, plants from four localities in Yunnan and Guizhou are all tetraploids. So it also has probably been formed from widespread tetraploid *Calamagrostis* species. Its short glumes should have derived from equal glumes of *Calamagrostis*, not from different origin.

The case of *D. neglecta* is much more complicated. *D. neglecta* is recognized by Soreng (2003) as a synonym of *C. stricta* (Timm) Koeler but as a different species by Chen (2001) and Lu *et al.* (unpublished manuscript for Flora of China, English edition). Some cytological studies have been done under the name *D. neglecta* and *C. stricta* respectively. For *D. neglecta*, tetraploids were found in North Europe (Engelskjön, 1979), octoploids ($2n = 56$), decaploids ($2n = 70$), and dodecaploids ($2n = 84$) were found in Russia (Sokolovskaya and Probatova, 1977). For *C. stricta*, tetraploids ($2n = 28$) were found in southwestern Finland (Aronhka, 1982), northern England (Crackles, 1994), and west Greenland (Dalgaard, 1988), dodecaploids ($2n = 12x = 84$) were found in Japan (Tateoka, 1976), and aneuploids ($2n = c. 104, 114, 116, 119, 120, 123$) were found in Eastern North America (Greene, 1984). If *D. neglecta* is a synonym of *C. stricta*, the species is distributed in Eurasia and Americas. From the chromosomal studies, we can assume that it has been formed in Europe, where many tetraploids have been found, and has spread through Asia to North America. In high mountains or cold regions of Asia to North America, polyploidization and hybridization may have occurred in the species to adapt the environmental or climate changes, therefore hexaploids, dodecaploids and aneuploids are found in these areas. If *D. neglecta* is a different species from *C. stricta*, *D. neglecta* is only distributed in Eurasia and the chromosomal reports of it are not enough to make a conclusion. Therefore careful morphological study for *D. neglecta* and *C. stricta* is needed to elucidate their relationship. For this widespread species, this study is only to add a report for the species and no further conclusion can be made on the hexaploid plants we studied. However, it is noticeable that the population we studied in China, though a hexaploid, exhibits typical morphology of *D. neglecta*,

not integrated with characters of other species, so it is certain that it is from the tetraploid and octoploid plants of the species, not a hybrid with other species.

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