

Chromosome Numbers in Gymnosperms - An Update

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Abstract

The present report is based on a cytological data base on 614 (56.0 %) of the total 1104 recognized species and 82 (90.0 %) of the 88 recognized genera of gymnosperms. Family Cycadaceae and many genera of Zamiaceae show intrageneric uniformity of somatic numbers, the genus *Zamia* is represented by a range of number from $2n=16-28$. *Ginkgo*, *Welwitschia* and *Gentium* show $2n=24$, $2n=42$, and $2n=44$ respectively. *Ephedra* shows a range of polyploidy from $2x-8x$ based on $n=7$. The family Pinaceae as a whole shows $2n=24$ except for *Pseudolarix* and *Pseudotsuga* with $2n=44$ and $2n=26$ respectively. Araucariaceae constantly shows $2n=26$ while Podocarpaceae has a range of $2n=18-38$. Sciadopityaceae and Cupressaceae are represented by $2n=20$ and $2n=22$ respectively. Taxaceae shows variable numbers of $2n=24$, 36 and 22. Polyploidy is exceptional being represented by 8.0 % of the taxa studied. B-chromosomes have been studied in 31 taxa while heteromorphic sex chromosomes have been reported in some dioecious taxa.

Keywords: *gymnosperms, chromosome numbers, polyploidy, B-chromosome, sex chromosomes*

Introduction

Gymnosperms are a small close knit group of seed plants with significantly less species diversity as compared to angiosperms. Nevertheless, they constitute 39 % of world's forests in both the hemispheres (Armenise et al. 2012) and their importance in regulating global carbon cycles, supply of timber, resins, edible nuts and in horticulture cannot be overstated (Zonneveld 2011, Farjon 2018). As a group, however, there is

still some controversy with regard to a monophyletic or paraphyletic origin of the gymnosperms (Hill 2005). Recently they have been classified into four subclasses Cycadidae, Ginkgoiidae, Gnetidae and Pinidae under the class Equisetopsida (Chase and Reveal 2009) comprising 12 families and 83 genera (Christenhusz et al. 2011) and 88 genera with 1104 recognized species according to the Plant List (www.theplantlist.org). The validity of accepted name of each taxa and the total number of species in each genus has been checked from the Plant List (www.theplantlist.org). The chromosome numbers of 688 taxa arranged according to the recent classification (Christenhusz et al. 2011) have been summarized in Table 1. The cytological data have been obtained from Chromosome Counts Database (CCDB), Index to Plant Chromosome Numbers (IPCN), Mehra (1988), and over 600 original references, listed separately for each genus in the data base.

Chromosome number data

The present study is based on a very comprehensive chromosome and genome size data base of gymnosperm species, prepared by the authors. The last compilation of chromosome numbers was done some 60 years back (Khoshoo 1961), a large amount of data has accumulated since then resulting in the representation of 82 genera and 688 taxa comprising of 614 species which is well above that of any other plant group. These data representing 56.0 % of the species and 90.0 % of the genera have provided further insight into the cytological information of this important group of plants. All the gymnosperm genera except *Columbea*, *Austrotaxus*, *Callitropsis*, *Neocupressis*, *Sabina* and *Margbansonia* are represented in Table 1. The range of chromosome numbers is rather narrow from $2n=14-66$ showing a 5-fold variation (Table 1, Fig. 1) as compared to angiosperms from $2n=4$ -ca.640 a 160-fold variation (Johnson et al. 1989). Another significant feature is the occurrence of a constant basic number in most of the individual families.

Table1
Chromosome numbers in Gymnosperms

Sr. No.	Taxon	Total No. of Species	Chromosome Number (No. of taxa Counted)
	Subclass I.: Cycadidae		
	Order A: Cycadales		
	Family: Cycadaceae		
1.	<i>Cycas</i>	92	22 (31)
	Family Zamiaceae		
2.	<i>Dioon</i>	13	18 (10)
3.	<i>Bowenia</i>	2	18 (2)
4.	<i>Macrozamia</i>	39	18 (15)
5.	<i>Lepidozamia</i>	2	18 (2)
6.	<i>Encephalartos</i>	68	18 (23) 27(1 plant, <i>E. hildebrandtii</i>)
7.	<i>Stangeria</i>	1	16 (1)
8.	<i>Ceratozamia</i>	25	16 (13)
9.	<i>Microcycas</i>	1	26 (1)
10.	<i>Zamia</i>	65	16-28 (41)
	Order B: Ginkgoales		
	Family: Ginkgoaceae		
11.	<i>Ginkgo</i>	1	12 (haploid), 24, 36, 48 (1)
	SUBCLASS III. GNETIDAE		
	ORDER C. WELWITSCHIALES		
	FAMILY WELWITSCHIACEAE		
12.	<i>Welwitschia</i>	1	42 (1)
	ORDER D. GNETALES		
	FAMILY GNETACEAE		
13.	<i>Gnetum</i>	41	44 (3), 44, 48 (1)
	ORDER E. EPHEDRALES		
	FAMILY EPHEDRACEAE		
14.	<i>Ephedra</i>	70	14 (16), 28 (18), 42 (2), 42, 56 (1), 28, 56 (1), 56 (1), 14, 28 (8), 1 with Bs
	SUBCLASS IV. PINIDAE		
	ORDER F. PINALES		
	FAMILY PINACEAE		
15.	<i>Cedrus</i>	3	24 (4)
16.	<i>Pinus</i>	130	24 (103), 36, 48 (1 sporadic), 48 (2 sporadic), 1 with B
17.	<i>Cathaya</i>	1	24 (1)
18.	<i>Picea</i>	40	24 (37), 36, 48 (2 sporadic), 19 with Bs
19.	<i>Pseudotsuga</i>	4	24 (4), 26 (2)
20.	<i>Larix</i>	14	24 (17), 36 (1 sporadic), 48 (1 sporadic), 1 with B
21.	<i>Pseudolarix</i>	1	44 (1)
22.	<i>Tsuga</i>	10	24 (10)
23.	<i>Nothotsuga</i>	1	24 (1)
24.	<i>Keteleeria</i>	3	24 (4)
25.	<i>Abies</i>	48	24 (33), 48 (1 sporadic), 36, 48 (1 sporadic)
	Order: Araucariales		
	Family 8: Araucariaceae		
26.	<i>Araucaria</i>	19	26 (20)
27.	<i>Wollemia</i>	1	26 (1)
28.	<i>Agathis</i>	18	26 (3)
29.	<i>Columbea</i>	1	--
	Family9: Podocarpaceae		
30.	<i>Phyllocladus</i>	4	18 (4)
31.	<i>Lepidothamnus</i>	4	28 (1), 30 (2)
32.	<i>Prumnopitys</i>	9	36 (1), 38 (2)
33.	<i>Sundacarpus</i>	1	38 (1)
34.	<i>Halocarpus</i>	3	18 (1), 22 (1), 24 (1)
35.	<i>Parasitaxus</i>	1	36 (1)
36.	<i>Lagarostrobos</i>	1	30 (1)
37.	<i>Manoao</i>	1	20 (1)
38.	<i>Saxegothea</i>	1	24 (1)

Table 1: continued

Sr. No.	Taxon	Total No. of Species	Chromosome Number (No. of taxa Counted)
39.	<i>Microcachrys</i>	1	30 (1)
40.	<i>Pherosphaera</i>	2	26 (2)
41.	<i>Acropyle</i>	2	20 (2)
42.	<i>Dacrycarpus</i>	9	20 (3)
43.	<i>Dacrydium</i>	22	20 (9)
44.	<i>Falcatifolium</i>	6	20 (1)
45.	<i>Retrophyllum</i>	5	20 (3)
46.	<i>Nageia</i>	6	26 (2), 26, 20 (1)
47.	<i>Afrocarpus</i>	5	24 (3)
48.	<i>Podocarpus</i>	108	22 (1), 33 (1), 34 (2), 36 (1), 38 (3), 20, 22 (2), 34, 36 (1), 34, 35, 36 (1), 33, 34, 38 (1), 37, 38 (2)
49.	<i>Margbensonia</i>	1	---
	ORDER H. CUPRESSALES		
	FAMILY 10. SCIADOPITYACEAE		
50.	<i>Sciadopitys</i>	1	20 (1)
	FAMILY 11. CUPRESSACEAE		
51.	<i>Cunninghamia</i>	2	22 (2), 33 (1 sporadic), 1 with B's
52.	<i>Taiwania</i>	1	22(1), 33 (1 sporadic), 1 with B's
53.	<i>Athrotaxis</i>	3	22 (3)
54.	<i>Metasequoia</i>	2	22 (1), 1 with Bs
55.	<i>Sequoia</i>	1	66 (1), 1 with Bs
56.	<i>Sequoiadendron</i>	1	22 (1)
57.	<i>Cryptomeria</i>	1	22 (1), 33 (1 sporadic),
58.	<i>Glyptostrobus</i>	1	22 (1), 33 (1 sporadic)
59.	<i>Taxodium</i>	2	22 (3), 1 with Bs
60.	<i>Papuacedrus</i>	1	22 (1)
61.	<i>Austrocedrus</i>	1	22 (1)
62.	<i>Libocedrus</i>	5	22 (1)
63.	<i>Pilgerodendron</i>	1	22 (1)
64.	<i>Widdringtonia</i>	4	22 (4)
65.	<i>Diselma</i>	1	22 (1)
66.	<i>Fitzroya</i>	1	44 (1)
67.	<i>Callitris</i>	15	22 (6)
68.	<i>Actinostrobus</i>	3	22 (1)
69.	<i>Neocallitropsis</i>	1	22 (1)
70.	<i>Thujopsis</i>	1	22 (1)
71.	<i>Thuja</i>	5	22 (5)
72.	<i>Fokienia</i>	1	22 (1)
73.	<i>Chamaecyparis</i>	5	22 (7)
74.	<i>Cupressus</i>	19	22 (22), 22, 44 (2), 44 (1), 4 with B's
75.	<i>Juniperus</i>	75	22 (71), 22, 33 (1), 33, 44 (1), 22, 33, 44 (1), 22, 44 (7), 44 (9), 22, 44, 66 (1), 22, 66 (1)
76.	<i>Calocedrus</i>	4	22 (3)
77.	<i>Tetraclinis</i>	1	22 (1)
78.	<i>Platycladus</i>	1	22 (1) 33, 44 (Sporadic)
79.	<i>Microbiota</i>	1	22 (1)
80.	<i>Callitropsis</i>	1	---
81.	<i>Neocuprois</i>	3	---
82.	<i>Sabina</i>	2	---
	Family 12: Taxaceae		
83.	<i>Pseudotaxus</i>	1	24 (1)
84.	<i>Taxus</i>	9	24 (10), 16 (1), 1 withBs
85.	<i>Cephalotaxus</i>	8	24 (6)
86.	<i>Amentotaxus</i>	6	36 (1), 14, 40, 36 (1)
87.	<i>Torreya</i>	6	22 (4)
88.	<i>Austrotaxus</i>	1	---

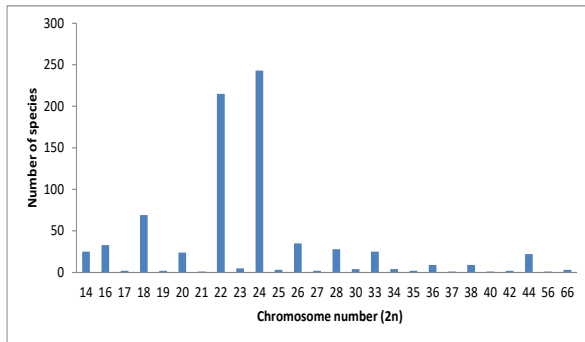


Fig. 1
Distribution of 2n chromosome numbers in 688 taxa of gymnosperms

Cycadaceae: Out of the total of 92 species, 31 species of *Cycas* studied show 2n=22 (Table 1).

Zamiaceae: This family with nine genera shows variable chromosome numbers. The cytologically studied species of *Dioon* (10 spp.), *Bowenia* (2 spp.), *Macrozamia* (15 spp.), *Lepidozamia* (2 spp.), *Encephalartos* (23 spp.) have 2n=18, *Stangeria* (1 sp.), *Ceratozamia* (13 spp.) have 2n=16 while *Microcycas* shows 2n=26 (Table 1). However, *Zamia* with 41 species studied shows a dysploid range from 2n=16-28 while *Z. chigua* (2n=22, 24, 25, 26; Norstog 1980, 1981), *Z. herrerae* (2n=23, 24; Nicolalde-Morejon et al.2009), *Z. lacandona* (2n=16, 17, 18; Schutzman & Vovides 1998), *Z. loddigesii* (2n=17,18 24-27; Moretti & Sabato 1984, Moretti 1990, Tagashira & Kondo 1999, 2001, Vovides & Olivares 1996), *Z. paucizuga* (2n=19, 23, 25, 27, 28; Napalitano et al. 2004), *Z. prasina* (2n=22, 26; Moretti et al. 1993) and *Z. variegata* (2n=21, 22; Moretti et al. 1991, 1993) show extensive intraspecific variation (Table 1). All this variability in chromosome numbers without any change in the number of chromosome arms is however, explained by centric fissions as there exists a ratio of one-to-two between median and terminal chromosomes with increase or decrease of somatic number (Olson & Gorelick 2011, Rastogi & Ohri 2019).

Ginkgoaceae: This monotypic family with *Ginkgo biloba* has 2n=24 (Table 1).

Welwitschiaceae: The only species *Welwitschia mirabilis* with 2n=42 has a unique all telocentric karyotype (Khoshoo and Ahuja 1963).

Gnetaceae: Four species of *Gnetum* i.e., *Gnetum gnemon*, *Gnetum montanum*, *Gnetum ula* and *Gnetum costatum* show 2n=44 (Table 1).

Ephedraceae: *Ephedra* shows a range of somatic numbers from 2n=14-56 among 47 species studied. The ploidy level goes up to octoploidy which is the highest among gymnosperms (Table 1).

Pinaceae: Among 11 genera included in this family *Cedrus*, *Pinus*, *Cathaya*, *Picea*, *Pseudotsuga* (except *P. menziesii*), *Larix*, *Tsuga*, *Nothotsuga*, *Keteleeria* and *Abies* constantly show 2n=24. *Pseudotsuga menziesii* shows a dysploid variation of 2n=26 and *Pseudolarix amabilis* has 2n=44. *P. menziesii* has a different karyotype of 10m+12sm+4t while 2n=24 species lack smaller telocentrics and instead have an additional metacentric pair which shows that increase in number is due to centric fission in a

metacentric pair (Christiansen 1963, El-Kassaby et al. 1983, Hizume & Kondo 1992, Hizume & Akiyama 1992). The CMA banding pattern of *P. menziesii* however, does not allow any derivation from 2n=24 species studied by Hizume & Kondo (1992). Similarly, *Pseudolarix amabilis* which shows 4 long sub-metacentrics and 40 small telocentrics of gradually decreasing size, derives its karyotype by centric fission of 20 sub-metacentrics (Mergen 1961, Hizume 2015).

Araucariaceae: Three genera investigated i.e. *Araucaria*, *Agathis* and *Wollemia* uniformly have 2n=26 (Table 1). There is no report for *Columbea*.

Podocarpaceae: Chromosome numbers of 19 species have been studied except for *Margbenosia* (Table 1). A variation of 2n=18-38 occurs in 19 genera and the karyotypes are characterized by various combinations of meta-, acro- and telocentric chromosomes resulting from centric fission (Table 1) (Hair and Beuzenberg 1958, Davies et al. 1997).

Sciadopityaceae: This monotypic family with *Sciadopitys verticillata* has a highly symmetrical complement of 2n=20 (Hizume 1989) (Table 1).

Cupressaceae: This family comprises 32 genera and except for *Callitropsis*, *Neocuprois* and *Sabina* which have not been investigated, the rest have constant basic number of x=11 (Table 1). Out of the 169 species studied 144 are diploid with 2n=22, intraspecific polyploidy is shown by 13 species and 12 species are exclusively polyploid (Table 1).

Taxaceae: Variable numbers are present i.e., 2n=24 (*Taxus* and *Cephalotaxus*), 2n= 40, 36, 14 (*Amentotaxus*) and 2n=22 (*Torreya*) (Table1). The report in *Amentotaxus* however, needs further verification. The only remaining genus is *Austrotaxus* which has not been investigated.

Polyploidy

As has been explained earlier, the cases of recent polyploidy are very less and exceptional in comparison to angiosperms (Khoshoo 1959, Ahuja 2005). The data obtained till now shows that out of 685 taxa known cytologically 5.0 per cent are polyploid 3.0 per cent have both diploid and polyploid types and the rest 92.0 per cent are diploid (Fig. 2). Polyploidy in the gymnosperms occurs in the form of stray seedlings, individual trees, intraspecific polyploidy in cultivation or in wild and entirely polyploid species and genera (Khoshoo 1959).

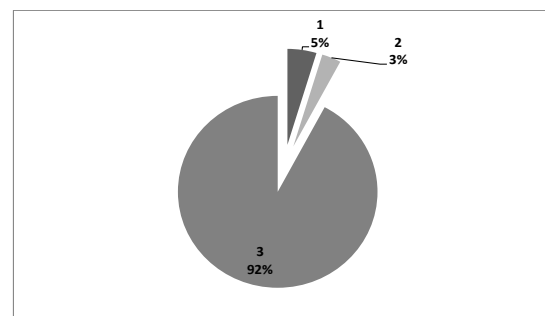


Fig. 2
Percentage of polyploids (1), intraspecific polyploids (2) and diploids (3) in 685 taxa of gymnosperms

In the entire Cycadidae a single case of a triploid individual is known in a cycad species *Encephalartos hildebrandtii* (Abraham and Mathew 1966).

Individual cases of polyploidy have been found in some Pinaceae i.e. *Pinus*, *Picea*, *Larix*, *Abies* and *Cupressaceae* genera i.e. *Cunninghamia*, *Taiwania*, *Cryptomeria*, *Glyptostrobus*, *Cupressus*, *Juniperus* and *Platyclusus* (Table 1).

Recently an extensive survey of 2200 individual trees which included seedlings obtained from a known tetraploid tree (Smarda et al. 2018) and 371 plants of 200 cultivars has shown a spontaneous origin of haploid, triploid and tetraploid individuals and named cultivars (Table 1), morphologically distinct from diploids, growing in semi-natural and cultivated state (Smarda et al. 2018). It is therefore stated that *Ginkgo biloba* spontaneously produces individuals at different ploidy levels in a frequency which is well above being sporadic or extremely rare, however these polyploid individuals while grow normally in cultivation, supposedly have low survival in wild (Smarda et al. 2018).

Ephedraceae and Cupressaceae have been recently found to have a high incidence of polyploidy than the cases earlier known. In Ephedraceae out of the total of 47 species studied, intraspecific polyploidy is detected in *Ephedra americana*, *E. chilensis*, *E. equisetina*, *E. fragilis*, *E. gerardiana*, *E. monosperma*, *E. przewalskii*, *E. regeliana* (2x, 4x), and exclusively polyploid species are *E. altissima*, *E. aspera*, *E. boelckeii*, *E. coryi*, *E. culteri*, *E. distachya*, *E. distachya* subsp. *helvetica*, *E. gerardiana* var. *sikkimensis*, *E. glauca*, *E. likiangensis*, *E. likiangensis* f. *mairei*, *E. lomatolepis*, *E. nevadensis*, *E. sinica*, *E. strobilacea*, *E. transitoria*, *E. trifurca*, *E. viridis* (4x), *E. californica* (6x, 8x), *E. funerea* (4x, 8x), *E. aphylla*, *E. sarcocarpa* (6x), *E. antisiphilitica* (8x) (Ickert Bond et al. 2014, Wu et al. 2016).

Similarly in Cupressaceae out of 169 species studied 13 show intraspecific polyploidy i.e. *Cupressus dupreziana*, *C. macrocarpa* (2x, 4x), *Juniperus chinensis* (2x, 3x, 4x), *J. chinensis* var. *sargentii*, *J. depeana* var. *gamboana*, *J. pingii*, *J. polycarpus* var. *seravschanica*, *J. sabina*, *J. squamata*, *J. squamata* f. *wilsonii* (2x, 4x), *J. foetidissima* (2x, 6x), *J. phoenicea* (2x, 4x, 6x) (Table 1). Exclusively polyploid species are *Sequoia sempervirens* (6x), *Fitzroya cupressoides*, *Cupressus guadalupensis* var. *forbesii*, *Juniperus coxii*, *J. indica*, *J. procumbens*, *J. przewalskii*, *J. recurva*, *J. sabina* var. *balkanensis*, *J. thurifera*, *J. thurifera* subsp. *africana*, *J. tibetica* (4x), *J. pfitzeriana* (3x, 4x) (Table 1). Interestingly, a rather high incidence of polyploidy is observed in *Ephedra* (64.0 %) (Wu et al. 2016) and *Juniperus* (21.0 %) (Farhat et al. 2019a, b) (Figs. 3,4).

Autotetraploidy has been deduced in *Fitzroya cupressoides* based on tetrasomic inheritance (Premoli et al. 2000). The karyotype studies in *Sequoia*, *Metasequoia* and *Sequoiadendron* have brought out distinct differences between the karyotype of *Sequoia* and that of other genera therefore precluding the derivation of *Sequoia* complement from that of its close relatives (Schlarbaum and Tsuchiya 1975, 1984a, b, Ahuja 2005, 2009). Meiotic configurations in *Sequoia* further depict an overwhelmingly large numbers of bivalents and some multivalents including hexavalents indicating a diploidized autohexaploid, autoallohexaploid or a segmental hexaploid genome

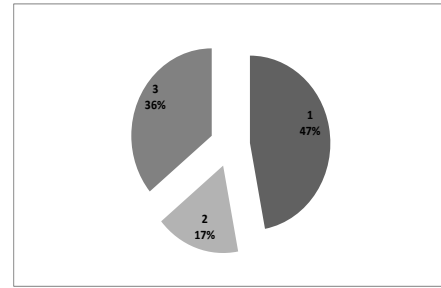


Fig.3 Percentage of polyplods (1), intraspecific polyplods (2) and diploids (3) in 47 taxa of *Ephedra*

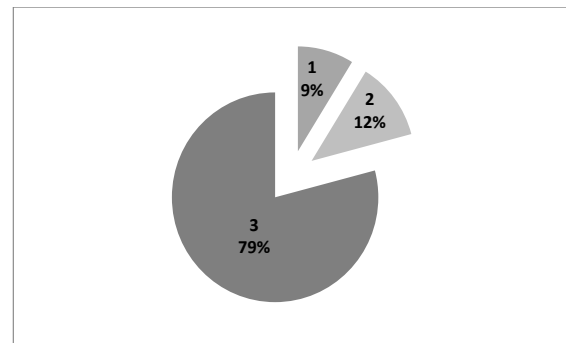


Fig.4 Percentage of polyplods (1), intraspecific polyplods (2) and diploids (3) in 91 taxa of *Juniperus*

(Ahuja & Neale 2002, Hizume et al. 2014, Ahuja 2009). Recently transcriptome data followed by Bayesian concordance analysis of single-copy genes strongly supported *Sequoiadendron* rather than *Metasequoia* as closest relative of *Sequoia* thereby discounting any genomic contribution from *Metasequoia*. However, the phylogenetic relationships based on single-copy genes do not exclude hybridization within *Sequoiadendron-Sequoia* clade therefore further evidence for autopolyploidy was obtained from orthogroups or homeologs of *Sequoia* as the duplicate genes show more similarity of sequences than expected (Scott et al. 2016). On the contrary, the interrelationships based on two single copy nuclear genes (LFY and DDB2) and two chloroplast DNA fragments reveal widespread interspecific hybridization followed by allotetraploidy in *Ephedra* species (Wu et al. 2016). Another exclusively 4x species, *Juniperus thurifera* shows diploidization of its genome in revealing two 35S rDNA sites similar to diploid species (Valles et al. 2015). Therefore, it is clear that recent cases of polyploidy are primarily seen in Cupressaceae and Ephedraceae and the present data shows that total incidence of polyploidy in gymnosperms is about 8.0 %.

B-chromosomes

Like polyploidy, B-chromosomes also occur in very low frequency as compared to angiosperms. Supernumerary chromosomes have been detected in 31 taxa which make up about 5

% of the total cytologically known taxa. Solitary cases are present in *Ephedra*, *Pinus*, *Podocarpus*, *Taxus*, *Cunninghamia* and *Pseudotsuga*. However, a tree with $2n=27$ in *Pseudotsuga menziesii* may well be a trisomic (Owens 1967). *Larix* and *Cupressus* show B-chromosomes in two and three taxa respectively. The greatest frequency of instances are seen in *Picea* where 18 taxa show B-chromosomes in varying numbers (Table 1) (Rastogi and Ohri 2019).

Sex chromosomes

Majority of the gymnosperm species (64.6 %) are dioecious represented by Cycadidae, Gnetidae, *Ginkgo* and some species in Pinidae and the rest are hermaphrodite monoecious (Ohri & Rastogi 2019). Therefore, in dioecious taxa many studies have tried to show sex determination based on heteromorphism of sex chromosomes where either heteromorphic sex is male with XX/XY or female with ZZ/WZ system. In *Podocarpus* the male sex chromosome may even be formed by the fusion of two telocentrics giving rise to $X_1X_2X_1X_2/X_1X_2Y$ system. Some species of *Cycas*, *Zamia*, *Stangeria* and one each of *Ephedra*, *Podocarpus* and *Ginkgo* show heteromorphic sex chromosomes (Table 1). These studies nevertheless, require further detailed analyses and confirmation (Ohri and Rastogi 2019).

Conclusions

As a small group, gymnosperms are well represented for their chromosome numbers compared with angiosperms. The dysploid variation is present in *Zamia*, *Pseudotsuga*, *Pseudolarix* and in *Podocarpaceae* because of chromosomal fusion/fission which do not alter the chromosome arms but increase/decrease chromosome number. The chromosome numbers and karyotypes are however, conserved within various families. Recent studies have shown that this apparent uniformity of chromosome number and form is not commensurate with great variation in fluorescent bands and number and position of rDNA and other repetitive sequences studied by fluorescent in situ hybridization (FISH) (Rastogi and Ohri 2019, Ohri & Rastogi unpublished). Such studies need to be extended to species which need further investigation as this will not only facilitate identification of chromosomes in the complement but also help to describe the interrelationships in various taxa. Similarly, as compared to angiosperms, B-chromosomes have been found in a small percentage of species with a non-random distribution, having been mostly discovered in *Picea species* (Rastogi & Ohri 2019). This aspect needs further investigation as the adaptive value shown by B-chromosomes in some particular ecological niche as found in some cases, has implications in forestry. Similarly a majority of gymnosperm species are dioecious but heteromorphic sex chromosomes have been discovered in less than one percent of the species. This aspect needs to be further explored in view of the studies done in *Dacrydium dacrydioides* and *Manoao colensoi* where distinct differences observed in genome size among male and female plants could not be detected in their karyotypes (Ohri & Rastogi

2019). The present work therefore summarizes the chromosome numbers investigated presently with a view to bring out the gaps in our knowledge of this rather important group of seed plants.

Acknowledgements

We are grateful to DBT, Govt. of India, New Delhi for financial assistance. Thanks are also due to Pro-Vice-Chancellor and Dean Science and Technology Amity University Uttar Pradesh, Lucknow Campus for encouragement and support. Data Archiving Statement

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