B-Chromosomes in Gymnosperms

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Abstract

B-chromosomes show a non-random distribution in different taxa of gymnosperms. They are generally smaller and show similar centromeric position as the normal complement and are heterochromatic in nature and may show DAPI or CMA banding. They are generally devoid of any gene content, do not pair at meiosis and show accumulation through female line. They show incremental effect on genome size and some adaptive value in particular ecological conditions.

Keywords: : *B-chromosomes, gymnosperms, frequency, meiotic pairing, adaptive value*

Introduction

Supernumerary or B-chromosomes are dispensable components of genome as they can be absent in certain individuals of a population, they show lack of pairing with A chromosomes because of genetic differentiation, and non-mendelian inheritance due to meiotic drive (Jones &Houben 2003). The origin of Bs is still an enigma nevertheless, they are generally considered to arise from A chromosomes (Jones et al. 2008). A convincing case in this respect is that of *Plantago lagopus* in which a trisomic for chromosome 2 after undergoing structural changes and massive accumulation of 5SrDNA sequences acquires B chromosome like properties (Dhar et al. 2002). They have wide distribution, being known from about 1300 plant species (Camacho 2005). However, their distribution is non-random among various taxonomic groups (Jones et al. 2008). Their adaptive value is not well established but it is observed that they are more common in plants inhabiting suboptimal and extreme conditions (Kunakh 2010). It is generally considered that B's are more frequent in species with larger genomes than those with smaller genomes, however they show negative correlation with ploidy levels (Trivers et al. 2004). Nevertheless, these correlations are not commensurate with the occurrence of Bs in nearly 40 species of hardwoods which both have smaller genomes as well as chromosome sizes (see Jones 1995, Ohri 2015). Gymnosperms, which have much larger genomes show the incidence of B-chromosomes in 31out of a total of 633 species known cytologicaly, making up 5 % of the total (unpublished data). An account of B-chromosomes in gymnosperms has been given by Muratova (2018). The present account however, systematically deals with not only the presence but various other aspects including their structure, frequency and biological significance of B-chromosomes in this important group of seed plants having great forestry importance.

Distribution

The distribution of B-chromosomes is non-random (Table 1) as these are completely absent in subclass Cycadidae. Family Ephedraceae has a single case of *Ephedra major* showing 1-2 B chromosome. In Pinaceae there is a single report in *Pinus sylvestris* and two in *Larix*. However, 19 Picea species with Bs have been reported till now. In Podocarpaceae the single report of *Podocarpus macrophyllus* shows a maximum number of 7 Bs

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Table 1
B chromosmes in gymnosperms

Sr No.	Taxon	2n=	Reference
	Family:Ephedraceae		
1.	*Ephedra major*	14+0-2B	Chouhdry & Tanaka 1983, Chouhdry 1984
	Family:Pinaceae		
2.	*Pinus sylvestris*	24+1B	Muratova&Kruklis 1988
3.	*Picea × fennica*	24+1B	Sedelnikova et al. 2011
4.	*Picea abies*	24+0-4B	Tashev et al. 2014
5.	*Picea brachytylavar.complanata*	24+0-1B	Hizume et al. 1991
6.	*Picea breweriana*	24+0-1B	Vladimirova 2006,Sedelnikova et al. 2011
7.	*Picea crassifolia*	24+1B	Sedelnikova et al. 2011,
		24+2B	Hizume 2017
8.	*Picea engelmannii*	24+2B	Hizume 2017
		24+1B	Shibata & Hizume 2008
		24+1-2B	Teoh & Rees 1977
9.	*Piceaglauca*	24+1B	Nkongolo 1996, Hizume 2017
		24+0-2B	Butorina et al. 2001, Bogdanova 2005
		24+1-6B	Teoh & Rees 1977
10.	*Picea glehnii*	2n=24+0-2B	Hizume et al. 1988d
		24+0-5B	Muratova 2000, 2005, Muratova & Vladimirova 2001, Muratova et al. 2001, 2008, Sedelnikova et al. 2011
11.	*Picea jezoensis*	24+0-2B	Muratova 1997a, 2000, 2004, Vladimirova et al. 2003, Sedelnikova et al. 2011
		24+0-1B	Liu& Li 1985, Hizume et al. 1989b, Nkongolo 1999, Muratova 2005
		24+1-3B	Muratova et al. 2008
12.	*Picea jezoensis* subsp. *hondoensis*	24+0-2B	Hizume et al. 1989b, Hizume & Kukuzawa 1995, Shibata & Hizume 2008
13.	*Picea koyamae*	24+1B	Shibata & Hizume 2008, Sedelnikova et al. 2011, Hizume 2017
14.	*Picea likiangensis*	24+0-1B	Hizume 2017
15.	*Picea linzhienensis*	24+1B	Li et al. 2001
16.	*Picea meyeri*	24+2B	Liu & Li 1985, Lai et al. 1986
		24+0-2B	Xu et al. 1994
		24+0-1B	Vladimirova et al. 2003
		24+0-3B	Muratova2005, Muratova et al. 2008
17.	*Picea obovata*	24+1B	Medwedewa & Muratova 1987, Muratova 1997a, Hizume 2017
		24+0-2B	Muratova 2000, Muratova et al. 2001, Vladimirova 2002
		24+0-3B	Kruklis 1971, Pravdin et al. 1976, Vladimirova et al. 2003
		24+0-4B	Muratova 2005, Vladimirova 2005, Sedelnikova et al. 2011
18.	*Picea pungens*	24+1B	Sedelnikova et al.2011
19.	*Picea schrenkiana*	24+0-1B	Muratova et al. 2001, 2008, Muratova 2005, Sedelnikova et al. 2011
20.	*Picea sitchensis*	24+0-2B	Moir & Fox 1972, Brown & Carlson 1997, Hizume 2017
		24+0-3B	Moir and Fox 1976
		24+0-5B	Moir and Fox 1977, Kean et al 1982
21.	*Picea wilsonii*	24+1-2B	Liu & Li 1985, Yang et al. 1994
		24+1B	Shi & Wang 1994a
22.	*Larix gmelinii*	24+0-1B	Muratova 1995, 2000, Muratova et al. 2008, Sedelnikova et al. 2011
23.	*Larix sibirica*	24+0-1B	Muratova 2005,Muratova et al. 2007 Kvitko et al. 2009, Sedelnikova et al. 2011, Farukshina & Putennikhin 2004
	Family: Podocarpaceae		
24.	*Podocarpusmacrophyllus*	37, 37+7B, (male)	Hizume et al. 1988c
	Family :Cupressaceae		
25.	*Cunninghamialanceolata*	22+1-2B	Han et al. 1984, Fang & Hsu 1986, Chen & Ye 1985
26.	*Taiwaniacryptomerioides*	22+1B	Fang 1986
27.	*Metasequoiaglyptostroboides*	22+1B	Fang 1986
28.	*Sequoia sempervirens*	66+1B	Saylor & Simons 1970
		66+3B	Fozdar & Libby 1968, Hizume et al 2014
29.	*Taxodium distichum* var. *imbricatum*	22+2B	Huang & Hsu. 1984
30.	*Cupressus arizonicavar.glabra*	22+1-2B	Hunziker 1961
31.	*Cupressus arizonica* var. *nevadensis*	22+1-2B	Thomas & Goggans 1972
32.	*Cupressus guadalupensis*	22+1-2B	Thomas & Goggans 1972
	Family : Taxaceae		
33.	*Taxus canadensis*	24+1B	Dark 1932, Sax & Sax 1933

reported in gymnosperms. In Cupressaceae Bs have been studied in monotypic genera e.g. *Cunninghamia, Taiwania, Metasequoia, Sequoia*, and in one and three species of *Taxodium* and *Cupressus* respectively. Family Taxaceae also has a single report of *Taxus canadensis* (Table 1).

Size and Structure

B-chromosomes as observed in various species are much smaller than the smallest chromosome of A complement and generally metacentric or sub-metacentric in all the species studied (Table 1). The frequency of occurrence of these two types of Bs has been noted in *Picea sitchensis* where meta- and submetacentric Bs are 82.4 and 17.6 per cent respectively (Moir & Fox 1977). This is in accordance with earlier studies which show a similarity of morphology between A and B chromosomes of a species (Camacho 2005).

B-chromosomes in *Picea glauca* are facultatively heterochromatic because when present they form distinct chromocentres which even makes it possible to determine their number, however the constitutive heterochromatin is not indicated by Giemsa staining (Teoh & Rees 1977). In *Sequoia sempervirens* however, the B chromosome is euchromatic (Saylor & Simons 1970). Fluorescent banding has been studied in some *Picea* species and *Sequoia sempervirens*. While both CMA and DAPI bands are seen in *Picea glauca* other species show either DAPI or CMA bands (Table 2).

Table 2
Fluorescent staining of B chromosomes

Sr No	Species	Fluorescent banding		Reference
		CMA	DAPI	
1.	*Picea crassifolia*	-	-	Hizume 2017
2.	*Picea glauca*	+	-	Hizume 2017
3.	*Picea koyamae*	-	+	Hizume 2017
4.	*Picea likiangensis*	-	+	Hizume 2017
5.	*Picea obovata*	-	+	Hizume 2017
6.	*Picea sitchensis*	+	-	Hizume 2017
7.	*Picea glehnii*	-	+	Hizume 1988d
8.	*Pice ajezoensis*	-	-	Hizume et al. 1989b
9.	*Picea jezoensis* subsp. *hondoensis*	-	-	Hizume et al. 1989b, Hizume & Kukuzawa 1995
10.	*Sequoia sempervirens*	+	-	Hizume et al.2014

Frequency

As is evident from Table 3 Bs occur in a very small frequency in *Larix* species where *L. sibirica* and *L. gmelinii* show an incidence of 1.6 and 6.7 per cent respectively in the seedlings studied (Sedelinkova et al. 2011). However, in *Picea* species this frequency may be as high as 45.5 % in a population (Hizume et al. 1991), but there is negative correlation between the number of Bs in an individual and their frequency of occurrence in the population (Table 3).

Table 3
Per cent frequency of number of B's in different species

Sr No.	Species	No. of B's	Occurrence (%)	Reference
1.	*Larix sibirica*	1B	1.6	Sedelinkova et al 2011
2	*Larix gmelinii*	1B	6.7	Sedelinkova et al 2011
3.	*Picea obovata*	1B	11.0	Pravdin et al. 1976
		2B	6.0	Pravdin et al. 1976
		1B	20.8-25.9	Kruklis 1971
		2B	2.0-3.8	Kruklis 1971
		3B	1.8	Kruklis 1971
4.	*Picea glehnii*	1B	19.5	Hizume et al. 1988d
		2B	1.9	
5.	*Picea brachytyla var. complanata*	1B	45.5	Hizume et al 1991

Gene content

Many B chromosomes have been known to include rDNA genes (Jones 1995, Camacho 2005). In *Picea obovata* silver nitrate staining shows clear telomeric blocks indicating presence of active nucleolar organizers (Sedelinkova et al. 2011). However, in *Picea engelmanii, P. jezoensis* var. hondoensis and *P. koyamae* the FISH signals of neither 45S nor 5S rDNA have been observed (Hizume & Kukuzawa 1995, Shibata & Hizume 2008).

Meiotic pairing and transmission

Studies in *Picea sitchensis* show that Bs neither pair with each other nor with A chromosomes and at metaphase I and they are randomly distributed around equatorial plate (Kean et al. 1982). Controlled crosses performed in this species show that the transmission of Bs through the male parent does not show any significant gain or loss while there is marked accumulation through female line possibly by preferential segregation towards the pole producing single functional megaspore after second division (Kean et al 1982, Fox 1987).

Nucleotypic effects and adaptability

Since Bs are present in addition to the normal complement it is natural that they effect the genome size of an organism. Detailed studies in this respect have been made in *Picea glauca* (Teoh & Rees 1976, 1977). While no significant differences were found in 2C DNA amounts in 26 provenances without Bs (Teoh & Rees 1976) an incremental addition of 2.7 % of the total genomic DNA of A complementper B chromosome, was observed ultimately making up 16 % of the genome size for the maximum of 6 Bs found in this species (Teoh & Rees 1977). Such increase in DNA amounts has been seen in many other cases as in maize it can be as high as 155 per cent (Rees 1974).

Some studies have been made on the effect of Bs on growth parameters and clinal variation in their frequency in different environments. In *Picea glauca* the Bs were found in 48 of the 51 populations studied and in 90 per cent of the plants. The study area was divided east to west by 95th meridian and it was found that the B frequency per plant in eastern maritime region was 2.25 times more than in western region and this variation coincided with rainfall pattern which was high in eastern provinces (130-150 cm per year) as compared to the northwest territories (25 cm per year). This shows that B frequency increases with increasing rainfall (Teoh & Rees 1977). This was corroborated further by providing artificial competition among young plants by growing them in conditions of different densities which confirmed differential mortality of plants with or without Bs under stress (Teoh& Rees 1977). Similar observations were made in *Allium schoenoprasum* where the seeds carrying Bs show germination advantage under drought conditions as compared to the ones without Bs (Holmes & Bougourd 1991). However, Moir and Fox (1976) found no major effect on growth rate related to Bs in *Picea sitchensis*. Such aspects concerning Bs in conifers might have strong implications in forestry and should be dealt with in detail.

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