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An Overview on Spruce Forests in China

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1. Introduction

The genus *Picea* A. Dietrich (spruce), which is a relative isolated group under evolution, belongs to Pinaceae family (Ran et al., 2006; Bobrow, 1970; Buchholz, 1929, 1931; Alvin, 1980; Mikkola, 1969). It includes 28–56 species depending on different systems of classification (Farjón, 1990; Ledig et al., 2004), most of which are in Eastern Asia, while many researchers thought that there were about 40 species in *Picea* genus and were only found in the north hemisphere (Budantsey, 1992, 1994; Wolfe, 1975, 1978; Tiffney and Manchester, 2001). The distribution range is from 21°N (Huanglian Mountains of Vietnam) to 70°N (Far Eastern area of Russia) (Fig. 1). Spruce forests are the main dominant vegetation in alpine coniferous forest in subtropical zone and temperate zone, and they are only found in alpine area, subalpine area and plateau from 21°N to 46°N (Li, 1995). In cold temperate zone and its adjacent regions (47°N to 57°N), spruce forests are the zonal vegetation types in boreal coniferous forest. From 57°N to 70°N, spruce forests transform from horizontal (latitudinal) zonal distribution to vertical (altitudinal) zonal distribution and from continuous distribution.

In the north of Euro-Asia continent, the main spruce species are *Picea abies* (L.) H. Karst. and *P. obovata* Ledeb., which form the continuous boreal coniferous forest (Ferguson, 1967; Florin, 1954, 1963; Guerli et al., 2001). *P. abies* is found in Alps of France, the Balkan Peninsula or the Balkan Mountains in the west, Germany and Scandinavian Peninsula in the north, Poland and the north and middle region of Russia in the east. In Siberian area of Russia, *P. obovata* takes the place of *P. abies*, it is found until to Lena River Valley and Okhotsk. But in the east Siberian area, *P. obovata* retreats from the dominant position, and is taken the place by *Larix sibirica* Ledeb. due to the rigorous continental climate (Colleau, 1968; Corrigan et al., 1978; Harris, 1979; Hart, 1987).

In North America, spruce species are abundant, including *P. glauca* (Moench) Voss, *P. mariana* (Mill.) Britton and al., *P. engelmannnii* Parry ex Engelm. and *P. sitchensis* (Bong.) Carriére (Barbour and Bilings, 1988; Klaus, 1987). *P. glauca* is distributed extensively in Canada and North USA, from Labradorian Peninsula and Alaska to Montana, North Dakota, Minnesota, Wisconsin, Michigan, to Massachusetts near Atlantic coast. *P. mariana* is

distributed almost in the whole Canada, and extensively in the eastern provinces and Newfoundland, to Alaska across Rocky Mountains in the west, and to Pennsylvania, north Virginia, Wisconsin, and Michigan in the south. Britain Colombia Province of Canada is the west border of *P. mariana*. *P. engelmannnii* is found in the west of North America, from Alberta Province and Britain Colombia Province of Canada to Arizona and New Mexico of USA along Rocky Mountains, it is also distributed in Cascade Range in Washington and Oregon. *P. sitchensis* distributes in the northwest of North America, and can be found from Aleutian Islands to Pacific coast of the northwest of California too (Delevoryas and Hope, 1973; Hsu, 1983; Weng and Jackson, 2000).

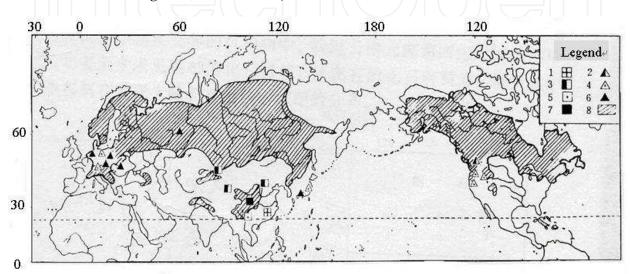


Fig. 1. The modern distribution range and fossil localities of *Picea* spp. in the world (based on Li, 1995, Lű et al., 2004, and McKenna, 1975) (1-7. Fossil localities: 1. Eocene; 2, 3. Oligocene; 4, 5. Miocene; 6, 7. Pliocene; 8. Modern distribution)

In China, the distribution range of spruce forests is very large, from Daxinganling Mountains (north) to Gaoligong Mountains (south), and Tianshan Mountains (west) to Central Mountains of Taiwan Province (east) (Fang, 1995, 1996; Fang and Liu, 1998). The spruce forests are found as long as there are site conditions of cold-temperate moisture types. In China the spruce forests belong to vertical zonal distribution with 17 species and 8 variations of *Picea* genus and take more than 40% of the species in the world. Furthermore, the almost all of the species are endemic in China, except for those in Daxinganling Mountains which belongs to East Siberian area and Arertai Mountains (belonging to West Siberian area). In China, spruce forests are distributed in Northeast, North, Northwest and Southwest.

In the mountains of Daxinganling, Xiaoxinganling and Changbai of Northeast China, *P. koraiensis* Nakai, *P. jezoensis* var. *microsperma* (Lindl. Cheng et L. K. Fu) and *P. jezoensis* var. *komarovii* (V. Vassil.) Cheng et L. K. Fu are the edificators of upland dark coniferous forests, which are extended partition of dark coniferous forests of Far East Area of Russia (Editorial Committee of Forest of China, 1997; Li, 1980; Li and Zhou, 1979).

The distribution range of spruce forest is restricted for drought in North and Northwest China. *P. meyeri* Rehder, E. H. Wilson and *P. wilsonii* Mast. are found in Jibei Mountains, Xiaowutai Mountains of Hebei Province, Guanqin Mountains, Wutai Mountains, Guandi

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Mountains of Shanxi Province in North China. In Northwest China, Arertai Mountains are the south border of *P. obovata*. *P. schrenkiana* var. *tianshanica* (Rupr.) Cheng et S. H. Fu is found in Tianshan Mountains, the west border of spruce forests in China. *P. crassifolia* Kom. Is distributed extensively in Qilian Mountains, Helan Mountains and Yinshan Mountains of Qinghai Province, Gansu Province and Ningxia Hui Nation Autonomous Region (Editorial Committee of Forest of China, 1997).

In Southwest China, including West Sichuan Province, north Yunnan Province and south Tibet Autonomous Region, there are 17 spruce species, which takes 43.3% of spruce species in the world. The important species are *P. likiangensis* (Franch.) E. Pritz., *P. likiangensis* var. *linzhiiensis* Cheng et L. K. Fu, *P. likiangensis* var. *balfouriana* (Rehd. et Wils.) Hillier ex Slavin, *P. purpurea* Mast., *P. brachytyla* (Franch.) E. Pritz., and so on, they form subalpine dark coniferous forests in Southwest China (Kuan, 1981; Sun, 2002; Wu et al., 1995).

P. spinulosa (Griff.) A. Henry and *P. smithiana* (Wall.) Boiss. are found in moist area in Himalayas in south Tibet Autonomous Region, and they always form small pure forest or mixed forest (Kuan, 1981).

P. morrisonicola Hayata forms the dominant pure coniferous forest in Central Mountains in Taiwan, which is the only subalpine coniferous forest of the east China in subtropical zone (Liu, 1971).

Monophyly of *Picea* has never been debated (Wright, 1955; Prager et al., 1976; Frankis, 1988; Price, 1989; Sigurgeirsson and Szmidt, 1993), but infrageneric classification of the genus remains quite controversial (Liu, 1982; Schmidt, 1989; Farjón, 1990, 2001; Fu et al., 1999), owing to morphological convergence and parallelism (Wright, 1955), and high interspecific crossability (Ogilvie and von RudloV, 1968; Manley, 1972; Gorden, 1976; Fowler, 1983, 1987; Perron et al., 2000). In addition, little is known about phylogenetic relationships of most species, especially the geographically restricted species growing in the montane regions of southwest China (LePage, 2001). Moreover, the origin and biogeography of *Picea* have drawn great interest from both geologists and biologists (Wright, 1955; Aldén, 1987; Page and Hollands, 1987; LePage, 2001, 2003), but they are still far from being resolved.

Spruce species are fine trees for lumbering, so researches on spruce were conducted very early in China (Editorial Committee of Vegetation of China, 1980). However, basic characteristics, flora, distribution types, and evolution relationship of the spruce species in China, and the relationship among spuce in China and abroad need more concern. There are many data about the topics above, but they are always scattered.

The aim of this study was (1) to summarize systematically the researches on spruce in China, and (2) to try to clarify the relationship among Chinese spruces, and among spruce in China and abroad.

2. Characteristics of species composition in spruce forests in China

2.1 The edificators in spruce forests in China

Picea spp. is distributed extensively in China (Editorial Committee of Forest of China, 1997). It is difficult to expatiate on the characteristics of edificators in spruce forests, so we divided China into five parts according to their districts, including Northeast China, Northwest

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<u>D: (: (</u>			D	DD		
District	Species	F	D	RD	Р	RP
Northeast	P. koraiensis	96.00	11.52	47.50	3.482	48.60
China	P. jezoensis var. microsperma	82.50	7.65	31.80	2.239	28.50
	Pinus korainensis Sieb.	47.50	1.56	4.29	0.626	5.21
	Populus davidiana Dode.	28.00	2.62	3.24	0.248	2.78
	Quercus mongolica Fischer ex Ledebour	16.50	2.13	1.87	0.104	1.67
	Betula platyphylla Suk.	32.50	1.19	2.61	0.182	2.36
	Betula ermanii Cham.	10.50	0.87	0.99	0.167	2.13
	Betula costata Trautv.	11.90	1.23	1.32	0.098	1.98
	Abies nephrolepis (Trautv.) Maxim.	31.75	2.95	2.45	0.204	3.11
	Larix gmelini (Rupr.) Rupr.	15.38	1.85	1.98	0.128	2.52
	Pinus sylvestriformis Taken.	9.82	0.62	0.23	0.075	0.85
Northwest	P. schrenkiana Fisch. et Mey.	88.50	11.00	35.65	4.457	42.80
China	P. schrenkiana var. tianshanica	75.00	9.88	29.54	4.023	32.60
	P. obovata	62.50	5.00	22.26	3.285	15.93
	Larix sibirica	28.00	1.61	3.28	0.241	2.75
	Betula pendula Roth.	15.50	0.95	1.06	0.113	0.82
	Sorbus tianschanica Mast.	9.20	0.43	0.95	0.108	0.36
	Populus talassica	11.42	0.87	0.62	0.168	1.55
	Betula tianschanica Cheng et S. H. Fu	8.75	0.65	0.53	0.201	1.10
North	P. meyeri	84.00	12.25	24.21	4.114	29.61
China	P. wilsonii	81.30	11.64	22.80	4.109	27.52
	P. asperata Mast.	67.50	9.58	15.21	2.628	14.20
	P. crassifolia	48.00	6.62	13.45	2.124	12.74
	Abies ernestii Rehd.	26.70	3.15	5.82	1.100	3.69
	Larix principis-rupprechtii Maryr.	22.58	2.69	4.63	0.482	2.37
	Pinus tabulaeformis Carr.	30.50	2.89	4.97	0.368	2.15
	Acer davidii Franch.	11.20	1.25	1.35	0.191	1.26
	Populus ningshanica L.	14.70	1.96	1.45	0.207	1.18
	Betula platyphylla	11.36	1.82	0.95	0.158	1.51
	Betula albo-sinensis Burk.	6.88	1.12	0.73	0.079	0.08
	Quercus liaotungensis Koidz	2.35	0.53	0.82	0.045	0.09
Southwest	P. likiangensis	65.40	12.27	17.23	3.885	17.62
China	P. likiangensis var. balfouriana	60.37	12.62	15.81	4.001	14.56
	P. purpurea	61.50	11.57	16.20	3.629	14.28
	P. asperata	45.22	5.68	9.45	2.156	9.76
	P. brachytyla	66.75	10.13	15.87	4.107	18.19
	P. brachytyla var. complanata Mast.	62.53	9.69	14.64	3.982	15.33
	Abies faxoniana Rehd. et Wils.	25.50	2.85	2.96	1.003	1.17
	Abies spectabilis (D. Don) Mirb.	21.23	4.23	2.35	0.691	2.21
	Pinus griffithii McClelland	17.79	3.91	1.46	0.268	1.28
	Pinus tabulaeformis	11.33	2.86	1.09	0.551	1.54
	Pinus armandii Franch.	7.83	2.15	0.78	0.079	0.08
	Populus davidiana	9.33	3.56	0.89	0.104	0.11
	Acer flabellatum Rehd.	6.74	3.54	0.34	0.073	0.08
	Quercus semicarpifolia Smith	8.12	2.31	0.28	0.097	0.08
	Betula platyphylla	9.92	1.75	0.34	0.162	0.09
	Betula utilis var. prattii D. Don	2.47	1.10	0.11	0.052	0.06
	Juglans cathayensis Dode	2.24	0.59	0.05	0.038	0.04

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Taiwan	P. morrisonicola	100.00	14.87	77.77	5.451	84.72
	<i>Tsuga chinensis</i> (Franch.) Pritz.	62.50	1.87	9.80	0.233	3.62
	Pinus armandii var. mastersiana (Hay.) Hay.	37.50	1.00	5.22	0.256	3.97
	Chamaecyparis obtuse var. formosana Matsum.	25.00	0.62	3.26	0.241	3.74
	Chamaecyparis formosensis Matsum.	12.50	0.12	0.65	0.002	0.02
	Cunninghamia konishii Hayata	12.50	0.12	0.65	0.085	1.31
	Trochodendron aralioides Sieb. et Zucc.	12.50	0.50	0.61	0.166	2.57

Table 1. Species characters in spruce forest in different districts in China (F-Frequency (%), D-Density (/100m²), RD-Relative density (%), P-Predominance, RP-Relative predominance (%))

China, North China, Southwest China and Taiwan. The characteristics of spruce forest in different districts in China are as shown in Table 1. In Northeast China, Northwest China and Taiwan, there are few edificators in spruce forests, while in North China and Southwest China, many species of spruce forests are found (Editorial Committee of Forest of China, 1997; Editorial Committee of Vegetation of China, 1980; Zhou, 1988; Chou, 1986, 1991).

2.2 Flora characters of spruce forests in China

In different districts in China, the floristic and geographical elements of spruce forests are complex (Table 2) (Wu, 1991; Wang, 1992, 2000). Generally speaking, there are more species belong to temperate zone element (Northeast China (83.39%), Northwest China (81.25%), North China (77.43%), Southwest China (72.50%), and Taiwan (70.66%)). In tropical China, spruce forest takes the following proportions: in North China (16.38%), Southwest China (22.92%), and Taiwan (24.50%). However, in temperate zone, spruce distribution in the three districts are as follows: North China (3.45%), Southwest China (2.08%), and Taiwan (2.28%)) are relatively less than the other two districts (Northeast China (8.15%) and Northwest China (10.41%)). China endemic elements in the three districts (North China (23.49%), Southwest China (37.92%), and Taiwan (32.19%)) are distinctly more than the other two districts are connected with other districts, such as northeastern Asia, Siberian, and Far East of Russia (Editorial Committee of Forest of China, 1997).

3. Section grouping based on cytogenetical studies

3.1 Karyotype of 17 Picea species in China

Karyotype is the basis of cladistics. We collected all the pictures on chromosome of different *Picea* species (Sudo, 1968; Hizume, 1988; Taylor and Patterson, 1980; von RudloV, 1967; Wang et al., 2000; Wu, 1985, 1987; Xu et al., 1994, 1998; Mehra, 1968). The pictures were treated by using the software Motic Images Advanced 3.0 to get the length of arms of chromosome. Researchers have found karyotype characters of 17 *Picea* species in China up to now (Table 3). Karyotype equations of these species include four types: 2n=24m, 2n=22m+2sm, 2n=20m+4sm, and 2n=16m+8sm. B chromosome is found only in *P. meyeri*, *P. wilsonii*, *P. jezoensis* var. *microsperma*, and *P. obovata*. There is no variation of chromosome number.

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Floristic	Geographical	Northeast	Northwest	North China	Southwest	Taiwan
types	elements	China	China		China	
I	(1)	15 (4.70)	15 (5.21)	22 (4.74)	18 (2.50)	9 (2.56)
II	(2)	21 (6.58)	13 (4.51)	12 (2.59)	14 (1.94)	8 (2.28)
	(3)	5 (1.57)	17 (5.90)	4 (0.86)	1 (0.14)	0 (0.00)
III	(4)	45 (14.11)	28 (9.72)	19 (4.09)	21 (2.92)	3 (0.85)
	(5)	46 (14.42)	36 (12.50)	54 (11.64)	43 (5.97)	32 (9.12)
	(6)	27 (8.46)	17 (5.90)	53 (11.42)	58 (8.06)	36 (10.26)
	(7)	42 (13.17)	12 (4.17)	32 (6.90)	49 (6.81)	18 (5.13)
	(8)	18 (5.64)	12 (4.17)	27 (5.82)	28 (3.89)	25 (7.12)
	(9)	34 (10.66)	23 (7.99)	109 (23.49)	273 (37.92)	113 (32.19)
	(10)	13 (4.08)	25 (8.68)	18 (3.88)	29 (4.03)	18 (5.13)
	(11)	9 (2.82)	25 (8.68)	11 (2.37)	8 (1.11)	0 (0.00)
	(12)	17 (5.33)	22 (7.64)	14 (3.02)	5 (0.69)	0 (0.00)
	(13)	15 (4.70)	34 (11.81)	13 (2.80)	8 (1.11)	3 (0.85)
IV	(14)	12 (3.76)	9 (3.13)	76 (16.38)	165 (22.92)	86 (24.50)
Total 5	14	319 (100.00)	288 (100.00)	464 (100.00)	720 (100.00)	351 (100.00)

Table 2. The floristic geographical elements of spruce forests in different districts in China (I World element ((1) World element), II Cold zone element ((2) North temperate zone-arctic element, (3) Siberia element), III Temperate zone element ((4) North temperate zone element, (5) Ancient world temperate zone element, (6) Temperate zone-Asia element, (7) East Asia element, (8) Sino-Japan element, (9) China endemic element, (10) Middle Asia element, (11) Aertai-Mongolia-Dahuri element, (12) Dahuri-Mongolia element, (13) Mongolia steppe element), IV Tropical zone element ((14) North temperate-tropical zone element))

No. Species		Karyotype	Arm ratio	Chromosome	Karyotype
	-1	equation		length ratio	type
1	P. asperata	20m+4sm	1.31 ± 0.04	1.71±0.32	1A
2	P. retroflexa Mast.	22m+2sm	1.24 ± 0.14	1.89±0.56	2A
3	P. koraiensis	20m+4sm	1.42 ± 0.23	1.72 ± 0.12	2A
4	P. meyeri	22m+2sm+2B	1.36 ± 0.15	1.77±0.29	2A
5	P. wilsonii	20m+4sm+1B	1.27±0.28	1.89±0.31	2A
6	P. schrenkiana	20m+4sm	1.38±0.29	1.83±0.42	2A
7	P. schrenkiana	16m+8sm	1.42 ± 0.18	2.12±0.18	2B
	var. tianshanica				
8	P. smithiana	20m+4sm	1.31±0.47	1.85±0.21	1A
9	P. morrisonicola	16m+8sm	1.50±0.33	1.87±0.34	2A
10	P. likiangensis	20m+4sm	1.27±0.18	1.60±0.19	2A
11	P. likiangensis	20m+4sm	1.34 ± 0.26	1.77±0.45	2A
	var. balfouriana				
12	P. purpurea	20m+4sm	1.28 ± 0.16	1.86±0.16	2A
13	P. jezoensis	22m+2sm+1B	1.35±0.28	1.82 ± 0.53	2A
	var. microsperma				
14	P. brachytyla	20m+4sm	1.34 ± 0.32	1.84 ± 0.37	2A
15	P. brachytyla	20m+4sm	1.36±0.17	1.99±0.42	2A
	var. complanata				
16	P. mongolica	20m+4sm	1.33±0.18	1.83±0.15	1A
17	P. obovata	24m+3B	1.35±0.27	1.87±0.28	2A

Table 3. Karyotype characters of 17 spruce species in China

For karyotype type, there are 3 1A types (including *P. asperata, P. smithiana* and *P. mongolica* W. D. Xu) and 1 2B type (*P. schrenkiana* var. *tianshanica*). The others are 2A types.

3.2 Structure variation of chromosomes and evolution hierarchy

We took arm ratio as x-coordinate, and chromosome length ratio as y-coordinate. All *Picea* spp. were drawn as shown in (Fig. 2a, b). The change range of arm ratio is from 1.23 to 1.50, and most of species (22) are from 1.25 to 1.35. The change range of chromosome length ratio is from 1.60 to 2.12, and only 14 species are from 1.75 to 1.85 (Wang et al., 1990).

Structure variation of chromosomes of Chinese *Picea* spp. (Fig. 2a) is more obvious than *Picea* spp. found in other parts of the world (Fig. 2b).

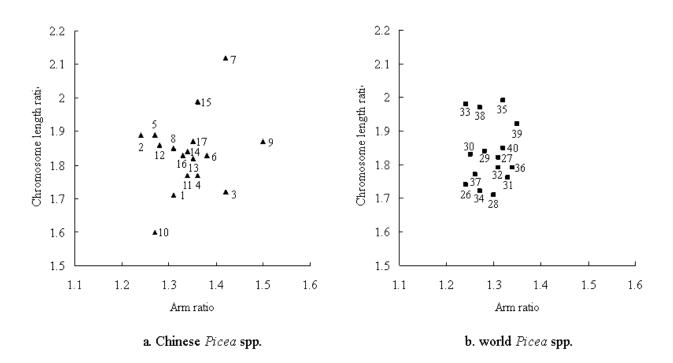


Fig. 2. Chromosomes structure of Chinese *Picea* spp. and other world *Picea* spp. (data based on Table 5)

Some researchers (Wang et al., 1990) thought a coefficient k (Karyotypic asymmetry in both average arm ratio and ratio of longest / shortest of chromosomes) was a good index for expressing the evolution hierarchy of certain species and genus.

$$k = \frac{A_i + L_i}{A_{\max} + L_{\max}} \times 100\% \tag{1}$$

Where A_i – average arm ratio of species (or genus), L_i – chromosome length ratio of species (or genus), A_{max} – maximum arm ratio in genus (or family), L_{max} – maximum chromosome length ratio in genus (or family).

According to value of k of *Picea* spp., the evolution hierarchy of 17 *Picea* spp. in China (Fig. 3) and 15 *Picea* spp. abroad (Fig. 4) were determined.

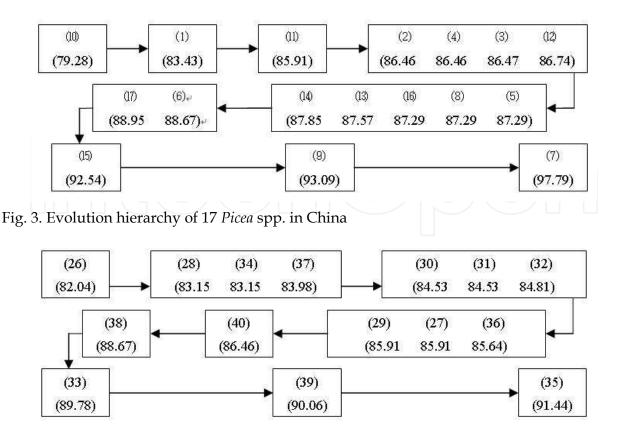


Fig. 4. Evolution hierarchy of 15 Picea spp. abroad

3.3 Section grouping

In taxonomy, *Picea* genus in China can be divided into three sections according to their karyotypes and the coefficient *k*. These sections are Sect. *Casicta*, Sect. *Omirica*, and Sect. *Picea*. Furthermore, we can determine their evolution hierarchy as in (Fig. 5) (Ran et al., 2006; Wu, 1991).

4. Distribution types of *Picea* spp. in China

4.1 Distribution range and niches of Picea spp. in China

The data of some *Picea* species (including *P. koraiensis, P. jezoensis* var. *microsperma, P. jezoensis* var. *komarovii*, and *P. mongolica*) are based on our previous field investigation. And we conducted the interpretation of TM image of some pivotal regions (including Tianshan Mountains in Xinjiang Weiwuer Autonomous Region, Hengduan Mountains in Sichuan Province and Tibet Autonomous Region, Qilian Mountains in Shaanxi Province and Gansu Province) (Liu et al., 2002; Yang et al., 1994; Editorial Committee of Forest of China, 1997; Cen, 1996).

4.2 Grouping of distribution types

Principal Components Analysis (PCA) was performed to compress the autocorrelated metric environmental variables by creating a reduced number of compounds (principal components) that explain the observed variation of distribution type (Jolliffe, 2002; Norusšis,

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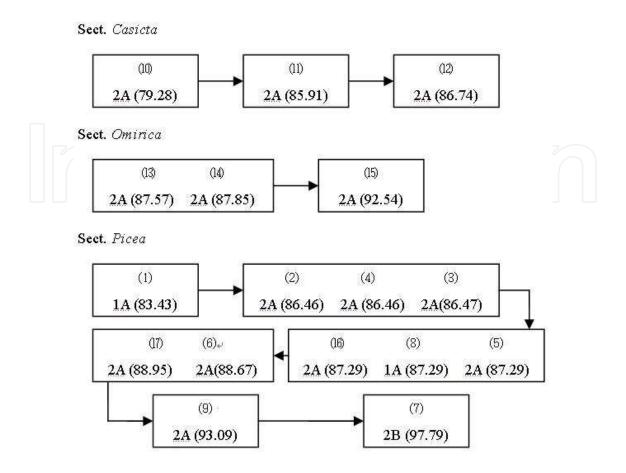


Fig. 5. Section grouping and evolution hierarchy of 17 Picea spp. in China

1990). Only compounds that accounted for more variation than any individual variable (eigenvalue > 1) were used in the final model. A 'varimax' rotation was applied to the reserved components to redistribute the variance among factors to obtain factor scores. Fuzzy clustering was then applied to the sample scores from the PCA ordination to identify the main distribution types. The fuzzy clustering specification used 3–6 clusters, a fixed fuzziness criterion of 2 and a convergence coefficient of 0.001. Then we obtained three categories of distribution types.

The first category is based on species adaptability to climate (mainly temperature, precipitation, and moisture). There are three types, including cold-moist type (10, 11, 12, 14, 15, 20, 22, 23, 25), cold-drought type (3, 6, 7, 13, 16, 17, 18, 19, 21, 24) and warm-moist type (1, 2, 4, 5, 8, 9).

The second category is based on environmental factors (particularly altitude). There are four types, including upland type (1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 14, 15, 18, 19, 21, 22, 23, 25), valley type (3, 13, 20), plain type (17, 24), and sandy land type (16).

The third category is based on distribution range (longitude and latitude) of species. There are three types, including narrow-distribution type (8, 9, 16, 17, 18, 22, 23, 25), medium-distribution type (1, 2, 4, 10, 11, 12, 14, 15, 21, 24) and broad-distribution type (3, 5, 6, 7, 13, 19, 20).

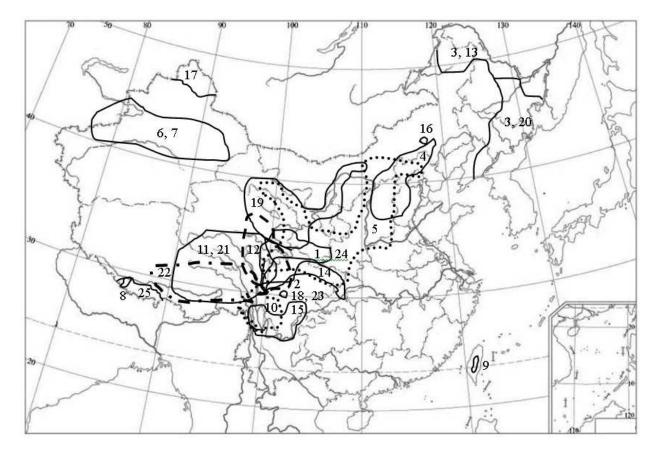


Fig. 6. The main distribution range of 25 Picea species in China

5. Discussion

5.1 The origin of Picea genus

Severe climatic oscillations associated with glacial cycles in the arctic during the late Tertiary and throughout the Quaternary era resulted in great changes in species distribution and population structure (Böhle et al., 1996; Qian and Ricklefs, 2000; Liu et al., 2002; Petit et al., 2003; Hewitt, 2004; Thomas, 1965). Meanwhile, descendent sea level created land connections for intercontinental exchanges of flora and fauna, especially boreal species (Tiffney, 1985a, b; Wen, 1999; Xiang et al., 2005). Spruce, as a kind of gymnosperm, is an archaic group under evolution, although pioneer reliable fossils of *Picea* genus are not available so early in Oligocene (Miller, 1975, 1977). Later in Oligocene and Miocene, fossils of *Picea* genus appear widely in Europe, North America and Japan (Page, 1988; Axelord, 1986, 1976; Ferguson, 1967). According to the fossils and modern distribution range, it can be concluded that ancestor of *Picea* genus might be a branch differentiate from Pinaceae during evolvement metaphase. But until Tertiary, ancient *Picea* spp. became the same as modern *Picea* spp.

Where does *Picea* genus originate from? There are many hypotheses in botanical science. Wright (1955) thought *Picea* genus might originate from northeastern Asia, and moved to North Arctic or diffused towards south along mountains. It seems logical because there are many *Picea* spp. there, including *P. jezoensis* var. *hondoensis* Mayr., *P. polita* Sieb. et Zucc., *P. jezoensis* Carr., *P. jezoensis* var. *microsperma*, *P. jezoensis* var. *komarovii*, *P. korainensis*. However, the hypothesis can not give a reasonable explanation to the phenomenon that

there are many *Picea* spp. in lower latitudinal regions in eastern Asia (Miller, 1988; Hopkins et al., 1994).

Wu (1991) thought the distribution center of *Picea* spp. was in East Asia, particularly in Hengduan Mountains according to his research findings. Li (1995) reported that in Hengduan Mountains, *Picea* spp. belonged to almost all of the subgroups except for an obvious evolutional subgroup – *P. pungens* subgroup originated from Rocky Range. In Hengduan Mountains in western Sichuan (Sun, 2002), northern Yunnan and eastern Tibet, there are more interspecific differentiations in *Picea* genus. Some species from Sect. *Picea* (*P. asperata, P. jezoensis,* and so on), Sect. *Casicta* (*P. likiangensis, P. likiangensis* var. *balfouriana,* and so on) and Sect. *Omirica* (*P. brachytyla, P. brachytyla* var. *complanata,* and so on) are found there. For example, in relatively ancient subgroup – Sect. *Picea,* there are 30 species and 2 variations in Sect. *Picea,* and 13 species and 1 variation are found here, which take 43.3% of the total species of Sect. *Picea.* So many researchers thought Hengduan Mountain was the original center of *Picea* genus, at least it was one of the most important differentiated centers.

It proved has been proven according to analysis on fossils and pollens of Picea genus (Jain, 1976; Miller, 1972, 1974, 1985; Schall and Pianka, 1978; Shi et al., 1998) that during the ice age in Quaternary, the forest composed of *Picea* spp. and *Abies* spp. and the two species were distributed widely in the mountains and plains of Southwest China, Northwest China, North China, East China, and Taiwan. During that time, cold-temperate coniferous forests have wider distribution range than present. It's well known that glacier activity was active in Quaternary, and vegetation zone moved in both horizontal and vertical directions. With the advance and retreat of ice sheets, species went extinct over large parts of their range, and some populations were dispersed to new locations or survived in refugia and then expanded again (Hewitt, 2000; Stewart and Lister, 2001; Abbott et al., 2000). This repeated process would on the one hand stimulate adaptation and allopatric speciation (Hewitt, 2004), whereas, on the other, provide the opportunities for hybridization between recolonized populations, even reproductively unisolated species (Abbott and Brochmann, 2003). During interglacial time, because of climate warming, some cold-temperate coniferous forests retreated to north, and others moved towards the mountains when the glacier melted, which formed the modern distribution range shrinking again and again. In Hengduan Mountains, there are more spaces and diverse habitats for cold-temperate coniferous trees moving upwards to the high environments (Sun, 2002). However, it's latitudinal is lower, so the cold-temperate coniferous species such as Picea spp. are distributed in the medium and top parts of mountains, which detached the distribution area into many parts, and some *Picea* spp. differentiate into many subspecies. The place became the center of geographical distribution and differentiation of *Picea* genus. The reticulate evolution and biological radiation resulted from climatic, ecological and geological changes broght many difficulties to the evolutionary and biogeographical studies of some taxa with long generation times, widespread distributions and low morphological divergence.

5.2 The relationship among Chinese *Picea* spp. and other world *Picea* spp.

Karyotype equations of 17 species of spruce in China include four types (2n=24m, 2n=22m+2sm, 2n=20m+4sm, and 2n=16m+8sm) (Table 3). Karyotype data of 15 species spruce abroad (Table 5) are shown (Hizume, 1988; Kinlaw and Neale, 1997; Niemann, 1979; Rushforth, 1987; Hilis and Ogllvie, 1970; Doyle, 1963), three of which are included in

Karyotype equations (2n=24m (*P. sitchensis*), 2n=22m+2sm (12 species), 2n=20m+4sm (2 species)).

No.	Species	Longitude (°)	Latitude (º)	Altitude (m)	Precipitation (mm)	Temperature (°C)	Moisture (%)
1	P. asperata	100.1-106.8	30.2-34.6	2400-3600	550-850	2-12	60-80
2	P. retroflexa	100.1-103.7	30-33.1	2100-4100	550-800	2-10	55-70
3	P. koraiensis	116.4-129	40.7-52.5	300-1800	600-900	2-4	60-80
4	P. meyeri	111.4-117.5	37.5-40.6	1400-2700	500-900	2-10	60-70
5	P. wilsonii	101.7-117.5	30-42.2	1400-2800	500-900	5-11	50-70
6	P. schrenkiana	75.2-95	37.7-45.6	1200-3000	500-600	-3-6	50-65
7	P. schrenkiana var. tianshanica	77-94.5	37-46	1250-3000	500-600	-3-5	50-70
8	P. smithiana	85.3	29	2300-3200	700-1000	6-13	50-70
9	P. morrisonicola	120.8-121.5	23.2-24.5	2500-3000	1000-1400	10-20	70-85
10	P. likiangensis	98.9-102.1	26.5-30.2	2500-3800	500-1100	0-9	60-80
11	P. likiangensis var. balfouriana	93.7-102.5	29.5-33.8	3000-4100	700-1100	2-8	70-80
12	P. purpurea	100.4-105.2	30.6-36.3	2600-3800	450-1100	0-6	60-80
13	P. jezoensis var. microsperma	124-134	41-52.5	300-1800	700-900	0-6	60-80
14	P. brachytyla	100.4-112	29.2-35.2	1500-3300	700-1100	2-9	60-80
15	P. brachytyla var. complanata	92-103.7	24.5-31.9	2000-3800	600-1100	0-9	60-80
16	P. mongolica	117.5	44.6	1100-1300	200-400	-2-2	30-60
17	P. obovata	86.5-90.5	46.7-48.6	1300-1800	400-600	-2-6	40-70
18	P. aurantiaca Mast.	102.1	30.2	2600-3600	600-700	-3-5	55-70
19	P. crassifolia	98.4-111.2	32.5-41	1600-3800	400-600	0-5	60-75
20	P. jezoensis var. komarovii	124-134	41-52.5	600-1800	700-900	0-6	60-80
21	<i>P. 1ikiangensis</i> var. <i>hirtella</i> Cheng et L. K. Fu	96.4-107.2	28.8-31.5	3000-4100	600-900	2-7	50-65
22	P. likiangensis var. linzhiensis	90.8-100.2	27.1-30.2	2900-3700	600-1000	4-9	55-70
	P. likiangensis						
23	var. <i>montigena</i> Cheng ex Chen	102.1	30.2	3300	600-700	-3-5	55-70
24	P. neoveitchii Mast.	102.5-110.8	31-34.6	1300-2000	400-600	3-8	50-70
25	P. spinulosa	85.2-89.1	27.8-29	2900-3600	450-900	0-8	60-75

Table 4. The distribution range and environmental factors of 25 spruce species in China

In Chinese *Picea* spp., B chromosome is found only in *P. meyeri*, *P. wilsonii*, *P. jezoensis* var. *microsperma*, and *P. obovata*. In **abroad** *Picea* spp., B chromosome is found only in *P. sitchensis*. There is no variation of chromosome number.

According to karyotypic asymmetry in both average arm ratio and length ratio of chromosomes, Chinese *Picea* spp. are more than that of abroad *Picea* spp. (Fig. 2, 10, 3, 9, 7). 2B karyotype is a relative evolutional type, and this type is only found in Chinese *Picea* spp..

Karyotype equation (16m+8sm) is a relative evolutional type, this type is not found in abroad *Picea* spp.. On the contrary, karyotype equation (24m), which is a relatively primordial chromosome, is found in them (*P. sitchensis*). We can conclude from karyotype structure that Chinese *Picea* spp. are relatively evolutional than abroad *Picea* spp.

No.	Species	Karyotype equation	Arm ratio	Chromosome length ratio	Karyotype type
26	P. abies	22m+2sm	1.24±0.33	1.74±0.34	2A
27	P. orientalis (L.) Link.	22m+2sm	1.31±0.42	1.82±0.24	2A
28	P. glauca	22m+2sm	1.30±0.21	1.71±0.19	2A
29	P. mariana	22m+2sm	1.28±0.09	1.84±0.53	7 1A
30	P. rubens Sarg.	22m+2sm	1.25±0.23	1.83±0.18	2A
31	P. engelmannii	20m+4sm	1.33±0.50	1.76±0.43	2A
32	P. pungens Engelm.	22m+2sm	1.31±0.11	1.79±0.12	2A
33	P. bicolor (Maxim.) Mayr.	22m+2sm	1.24 ± 0.12	1.98 ± 0.24	2A
34	P. glehnii (F. Schmidt) Mast.	22m+2sm	1.27 ± 0.24	1.72±0.18	2A
35	P. koyamae Shirasawa	20m+4sm	1.32 ± 0.08	1.99±0.45	2A
36	P. polita	22m+2sm	1.34 ± 0.48	1.79±0.29	2A
37	P. sitchensis	24m+2B	1.26±0.23	1.77±0.18	1A
38	P. omorika (Pančić) Purk	22m+2sm	1.27±0.12	1.97±0.57	2A
39	P. jezoensis	22m+2sm	1.35 ± 0.45	1.92±0.32	2A
40	P. jezoensis var. hondoensis	22m+2sm	1.32±0.09	1.85±0.18	2A

Table 5. Karyotype characters of 15 spruce species abroad

Hu et al. (1983) reported the differences of interspecific zymogram distances of genus *Picea* (Table 6). Firstly, concerning abroad *Picea*, *P. abies* is similar to the Chinese *Picea*, but it has long zymogram distance with *P. polita*. The zymogram distance between *P. polita* and other *Picea* except for *P. wilsonii* is long. The zymogram distance between *P. pungens* and other *Picea* except for *P. schrenkiana* and *P. wilsonii* is long. About the relationship between the Chinese *Picea*, the zymogram distances are short except for the following three pairs, those are *P. koraiensis* and *P. meyeri*, *P. meyerii* and *P. crassifolia*, *P. wilsonii* and *P. likiangensis*.

Species	P. abies	P. koraiensis	P. meyeri	P. crassifolia	P. schrenkiana	P. wilsonii	P. polita	P. likiangensis	P. pungens
P. abies	0	0.13	0.22	0.13	0.13	0.22	0.50	0.33	0.30
P. koraiensis		0	0.40	0.13	0.13	0.30	0.30	0.38	0.44
P. meyeri			7 o \	0.43	0.14	0.22	0.50	0.29	0.50
P. crassifolia				0	0.25	0.30	0.45	0.25	0.44
P. schrenkiana					0	0.13	0.40	0.14	0.22
P. wilsonii						0	0.20	0.43	0.20
P. polita							0	0.55	0.45
P. likiangensis								0	0.44
P. pungens									0

Table 6. Interspecific zymogram distances of *Picea* genus (Hu et al., 1983)

In zonal distribution, there are close contact among abroad *Picea* spp. and Chinese *Picea* spp., particularly, in Northwest China and Northeast China. In Northwest China, *P. schrenkiana* and *P. schrenkiana* var. *tianshanica* are distributed widely in Tianshan

Mountains. They diffuse towards west along Tianshan Mountains into mountains of Pakistan and Afghanistan. *P. obovata* distributes in Aertai Mountains in northern Xinjiang, and it is connected with Siberian region of Russia. In Northeast China, *P. koraiensis* is found in Da Xinganling Mountains, Xiao Xinganling Mountains, Wanda Mountains, Zhangguangcailing Mountains, and Changbai Mountains. It is also found in Korean Peninsula, and Far East of Russia (Zheng and Fu, 1978). *P. jezoensis* distributes widely in Northeastern Asia, including Far East of Russia, Korean Peninsula, and North Japan (Ying, 1989). When it extends into Northeast China, it differentiates into some variations, such as *P. jezoensis* var. *microsperma* (in Da Xinganling Mountains, Xiao Xinganling Mountains, Zhangguangcailing Mountains) and *P. jezoensis* var. *komarovii* (in Changbai Mountains). In North China, Southwest China, and Taiwan, the *Picea* spp. have few connection with abroad *Picea* spp., so there are many China endemic species in spruce forests of these regions.

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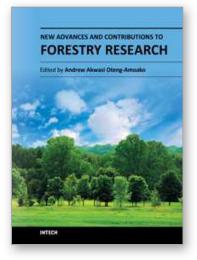
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