

Cone Morphological Variation of the *Picea jezoensis* Complex in Eastern Asia

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Abstract : *Picea jezoensis* with several infraspecific taxa is indigenous to Eastern Asia and the Far East of Russia. Although these taxa are very common, the taxonomic confusion surrounding this complex is reflected in ambiguity of the various taxonomic treatments currently used. Patterns of intraspecific variations of cone morphology and recognition of taxa within the *P. jezoensis* complex were investigated from 175 individuals. Morphological variation of cone characters was determined by the univariate analysis to be insignificant in separating most previously recognized infraspecific taxa in Korea, China, Russia, and Japan. Our statistical analysis showed that cones from northern populations were larger and wider than those from southern populations. Individuals from South Korea were predominantly smaller even than those from Honshu of Japan which were previously recognized as var. *hondoensis*. All measured characters appeared to show some clinal variation with changes in latitude, and a distinctive trend was evident. Consequently var. *hondoensis*, var. *koreana*, and var. *microsperma* cannot retain their infraspecific state within the *P. jezoensis* complex.

Key words : clinal variation, cone, marginal population, morphology, *Picea jezoensis*

Introduction

Jezo spruce, *Picea jezoensis* (Siebold et Zucc.) Carrière occurs in subalpine forests of the northern part of the Sikhote-Alin mountain range, the western coast of the Sea of Okhotsk, Mt. Chanbai, Shantar Islands, Sakhalin Island, the southern Kurils (Iturup and Kunashir Islands) and Hokkaido. Disjunct populations are found in the middle part of Honshu Island as *P. jezoensis* var. *hondoensis* (Mayr) Rehder, in central Kamchatka as *P. kamtchatkensis* Lacass., in southern Korea, and north-eastern China on the mountain range Dunlin, as *P. jezoensis* var. *komarovii* (V.N. Vassil.) W.C. Cheng et L.K. Fu (Lee, 1980; Farjon, 1990; Yamazaki, 1995; Fu et al., 1999; Krestov and Nakamura, 2002; Aizawa et al., 2007; Earle, 2008, see Figure 1).

Genus *Picea* A. Dietr is subdivided into two sections, *Picea* and *Casicta* Mayr., and sect. *Castica*, which is characterized by thin and flexible and loosely imbricate seed scales of cones with erose margins, comprises six

species in the world, i.e., *P. sitchensis* (Bong) Carrière, *P. likiangensis* (Franch.) Pritzl, *P. purpurea* Masters, *P. pungens* Engelm., and *P. engelmannii* Parry ex Engelm. including *P. jezoensis* (Farjon, 1990), although this treatment is not supported by a recent DNA study (Ran et al., 2006).

Information on the morphological variability of *Picea jezoensis* is fragmentary. *P. jezoensis* has not been critically revised, but the only floristic treatments are included in a diverse range of flora. Several varieties of *P. jezoensis* were proposed based just on the degree of twig color, cone size, and scale size using the northern part of the taxon's range (Wright, 1955; Ohwi, 1984; Charevicz, 1989; Farjon, 1990; Fu et al., 1999).

In China, Cheng and Fu (1978) recognized three infraspecific taxa, namely var. *microsperma* (Lindl.) W.C. Cheng et L.K. Fu, var. *komarovii* (V.N. Vassil.) W.C. Cheng et L.K. Fu and var. *ajanensis* (Lindl. & Gordon) W.C. Cheng et L.K. Fu based on cone shape and size, color of shoots, and leaf size. Also, var. *komarovii*, which exhibits the most restricted southern range, is characterized by smaller cones and yellowish first-year branchlets, and rhombic seed scales at middle of cones, compared with var.

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microsperma. On the other hand, var. *ajanensis*, which is distributed in northern part of Heilongjiang, is characterized by longer and narrower cones and brownish first year branchlets, compared with var. *microsperma*. However, Fu *et al.* (1999) recognized two infraspecific taxa, namely var. *microsperma* and var. *komarovii* mentioned only var. *jezoensis* as being distributed in Japan and eastern Russia without any indication of morphological distinction between var. *jezoensis* and two varieties in China.

In Korea Uyeki (1942) described var. *koreana* Uyeki as having small cone size and brown twigs. The circumscription of var. *komarovii* appears to be a synonym of var. *koreana* because of morphological identities and distribution. *P. jezoensis* var. *koreana* Uyeki has priority over *P. jezoensis* var. *komarovii*, which was described by Vassiljev (1950, not seen) and treated by Cheng and Fu as a variety (Cheng and Fu, 1978).

On the other hand, in Russia Gaussen and Lacassagne (1930) recognized three species in the Far East of Russia, *P. jezoensis*, *P. ajanensis* (Lindl. et Gordon) Fisch. ex Carrière, *P. kamtschatkensis*. Furthermore, Vasiljev divided *P. jezoensis* into three species, *P. microsperma* (Lindl.) Carrière, *P. komarovii* Vasiljev, and *P. komarovii* V.N. Vassil (Potenko, 2007b). Charkevicz (1989) and Farjon (1990) recognized *P. kamtschatkensis* as a synonym of either or *P. jezoensis*.

In Japan Elwes and Henry (1909) treated the Honshu individuals as specifically distinct, *P. hondoensis* Mayr, but Rehder (1940) and Hayashi (1969) reduced to an infraspecific taxon of *P. jezoensis*, i.e., *P. jezoensis* var. *hondoensis* (Mayr) Rehder due to small cone size and redish brown twigs (vs. yellowish brown twigs) with small leaves. Kitamura and Murata (1979) considered many conifer species as one polymorphic species without recognition of infraspecific taxa, while other taxonomists (Farjon, 1990; Fu *et al.*, 1999) treated this variation pattern at the rank of one or several infraspecific species based on cone size and twig color. The broad species concept (=sensu lato) like Kitamura and Murata (1979) was generally supported by Wilson (1916) and Ohwi (1984) due to continuous variation, but many local flora and authors still recognized infraspecific taxa within the *P. jezoensis* complex in eastern Asia.

Previous studies (Aizawa and Kaji, 2006) in Japan showed large variation in cone morphology within populations of *Picea alcoquiana* (Veitch ex Lindl.) Carrière. Aizawa and Kaji (2006) argued that the appropriate rank to assign these taxa might be controversial as to whether the differences were at the infraspecific level or at one polymorphic species level. Likewise some individuals of *P. jezoensis* could not be reliably identified and questions arose regarding the extent to which the taxa differ and the degree of isolation. Especially there has been lit-

tle investigation of *P. jezoensis* at its southern extreme, where its evolutionary history is poorly known.

The variation range of Russian and Chinese individuals of *P. jezoensis* in terms of cone length and width resides within that of Japanese individuals according to Ohwi (1984). Twig color of Japanese individuals was described either brown or yellow, which were often mentioned as a key characteristics of infraspecific taxon (Ohwi, 1984). Farjon (1990) and Gil *et al.* (2002) showed that seed cone morphology was a helpful trait for taxonomic purposes or genetic discrimination in conifers.

A major difficulty can be attributed to the use of minor differences in cone morphology for taxon definition, and consequently the differences used to distinguish taxa are far from consistent. The populations of the *P. jezoensis* complex are more or less isolated within the distribution range (Uyeki, 1926; Ohwi, 1984; Charkevicz, 1989; Fu *et al.*, 1999), and this spatial isolation can influence intraspecific differentiation. Several geographically isolated populations of *P. jezoensis* are found in Kamchatka of Russia, Honshu of Japan, and upper elevation of Korea Republic, such as Mts. Deokyu-san and Jiri-san (Uyeki, 1926). The process of differentiation is expected to be more significant in populations located far from the main geographical center of occurrence rather than inside the main range. Morphological variability within conifer species, however, may result from clinal variation and an extensive ecological range (Bongarten and Hanover, 1986; Palmer and Parker, 1990; Rehfeldt, 1991; Wells *et al.*, 1991; Standby *et al.*, 2009).

There is a clear need for a study of these taxa that go beyond the limited work thus far. The aims of our study were to 1) analyze the geographic variation of the *Picea jezoensis* complex, thereby making it possible to evaluate the amount of morphologic differentiation, and 2) test the validity of the infraspecific taxa. We were specifically interested in determining whether the variability within the *P. jezoensis* complex are primarily attributable to cone morphological discontinuities among the geographically isolated groups and whether a suite of morphological characters can consistently distinguish these taxa. The morphological traits of cones, specific and diagnostic for the infraspecific taxa of the *Picea jezoensis* complex, were used in this study.

Materials and Methods

1. Plant material

This morphological study of the geographic variation in the *Picea jezoensis* complex in Korea, China, Russia, and Japan is based on material collected in natural forests from 2005 to 2006. Sites were chosen to represent the range of the natural distribution and to cover the

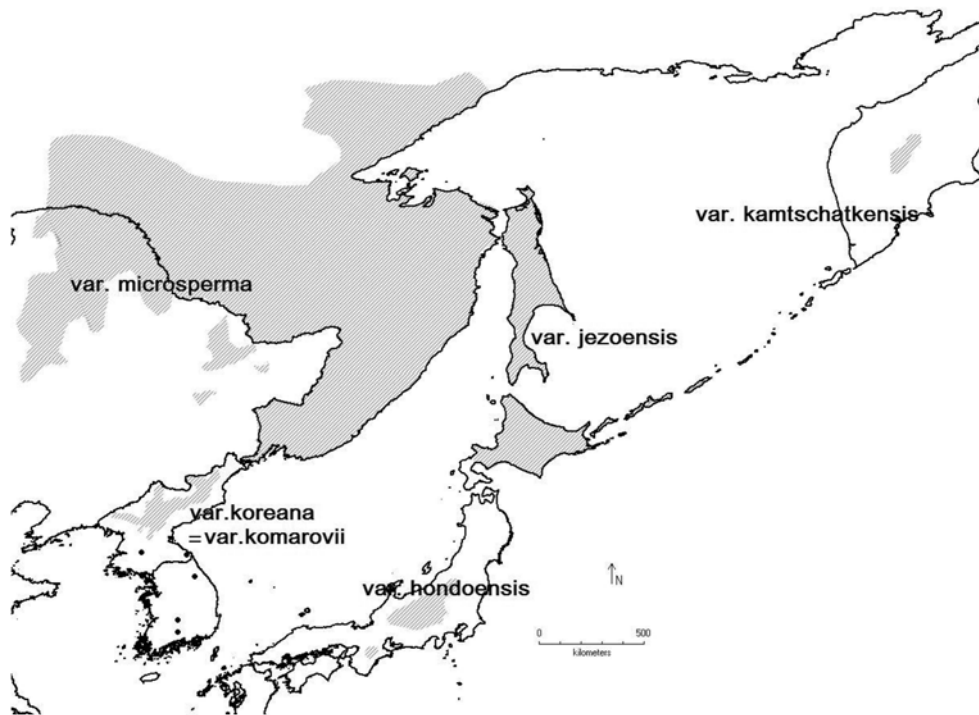


Figure 1. Geographical distribution of infraspecific taxa of the *Picea jezoensis* complex.

varieties described. Mature cones were collected from three localities, Mts. Jiri-san, Deokyou-san, and Gyeong-bang-san of Korea Republic, one locality of Hokkaido in Japan, one in northeastern China and one in the Far East of Russia. Representative specimens from the material collected were stored at T.B. Lee Herbarium of the Arboretum of Seoul National University (SNUA).

Herbarium material [University of Tokyo (TI), Tokyo Metropolitan University (MAK), Arnold Arboretum of Harvard University (A), and Chinese Academy of Sciences, Beijing (PE)] was also included in the analysis in order to test the validity of several varieties described and to improve the foundation for comparisons with the local taxa.

Prior to the morphological analysis, the specimens were tentatively referred to as *var. jezoensis* (individuals of Hokkaido, Japan and Russia), *var. hondoensis* (individuals of Honshu, Japan), *var. koreana* (Korean individuals), and *var. microsperma* (Chinese individuals) based on former taxonomic classification and geographic distribution.

2. Measurement of characters

Illustrations of the leaf and cone morphology (Figure 2) were adapted from Lee (1980). Characters considered useful by previous authors (Wilson, 1916; Kitamura and Murata, 1979; Lee, 1980; Ohwi, 1984; Yamazaki, 1995) for reliable identification were selected.

Certain features previously used in studies were omitted because they proved invariant among populations, e.g., leaf shape and length, twig color and pubescence, and bud shape.

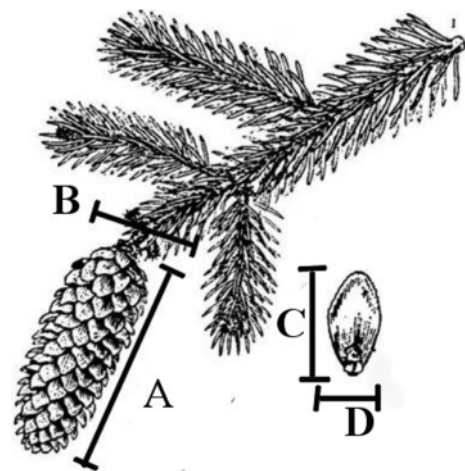


Figure 2. Diagram of *Picea jezoensis* with an indication of the measurement of the characters of cone and scale. A key to numbers is given in Table 1.

3. Data analysis

One hundred seventy five individuals (65 in Japan, 52 in China, 37 in Korea and 21 in Russia) for cones were assessed for four cone characters (Table 1 and Appendix). Patterns of morphological similarity/difference were analyzed by univariate statistical methods using the software package XLSTAT (release 5.5 A). Also, bivariate scatter diagrams were performed and characters associated with individuals in several taxa were plotted.

Measure cones were divided into size groups of length and width intervals which were estimated using histogram plots that show normal distributions. Normality

Table 1. Morphological characters for cone and scale of *Picea jezoensis* used in morphological analysis. Units of measurement were given in parentheses.

Code	Character
A	Cone length (cm)
B	Cone width (cm)
C	Scale length (mm)
D	Scale width (mm)

was tested by 95% confidence level using Shapiro-Wilk test (Palmer and Strobeck, 1992). We sought to determine what extent the characters might be polygenetic traits by this normal test and by exploring their relationship with latitude.

Results

Four cone characters were determined by the univariate analysis to be insignificant in separating most previously recognized infraspecific taxa in China, Russia, and Japan. Especially all the compared populations were more similar in scale length and width than in their cone length and width. Univariate statistics, in addition to the minimum and maximum values for scale length and width characters showed that values overlapped exten-

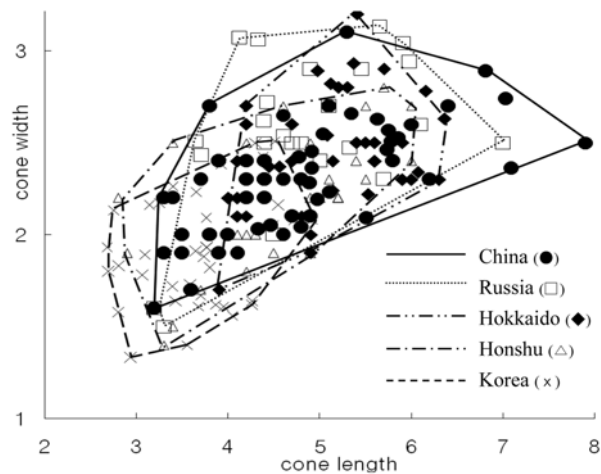


Figure 4. A scatter plot based on cone length vs. cone width and individuals sampled from Korea, China, Hokkaido, Honshu and Russia.

sively for all individuals of *P. jezoensis* (Figure 3).

Our statistical analysis showed that cones from northern populations are larger and wider than those from southern populations (Figure 4). Individuals from South Korea were predominantly smaller even than those from Honshu of Japan which were previously recognized as var. *hondoensis*, although much overlapped between Japanese Honshu and southern Korean individuals occurred in the central region of

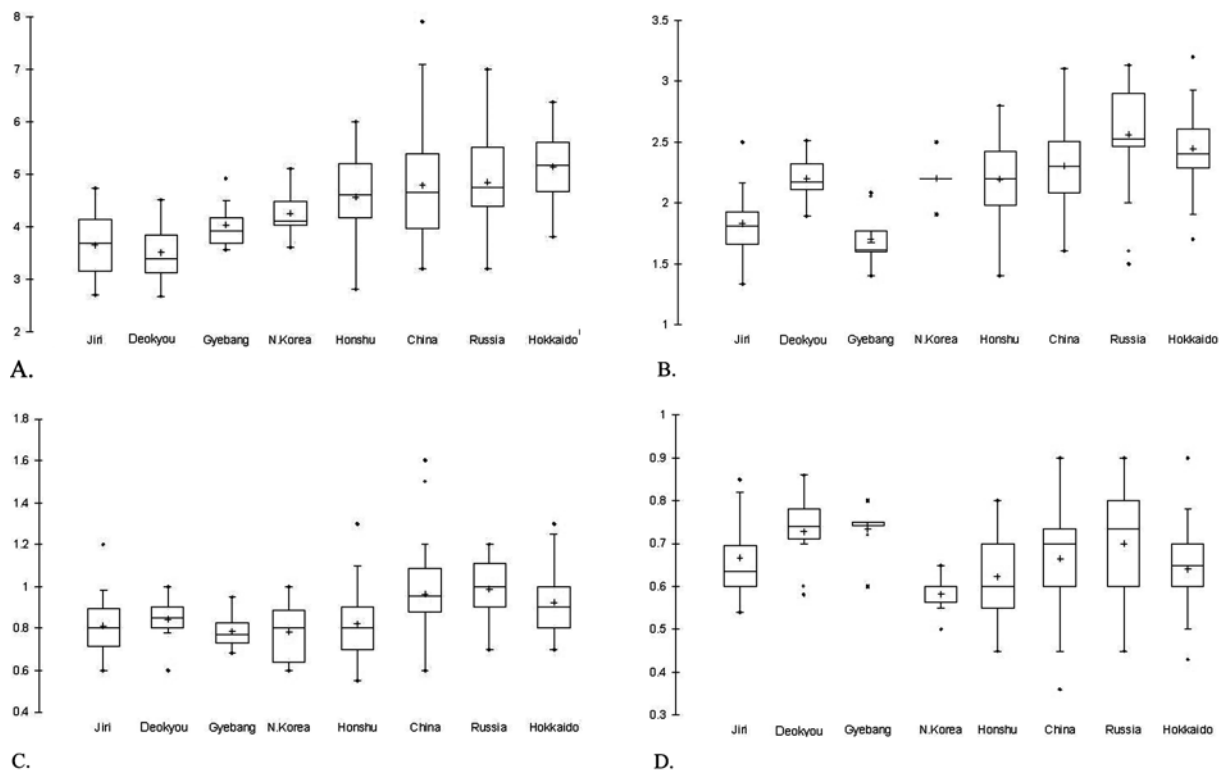


Figure 3. Univariate statistics with the minimum and maximum values for the discriminating characters for cone and scale of the *Picea jezoense* complex (var. *koreana*: Jiri, Deokyou, Gyeong and N. Korea; var. *hondoensis*: Honshu; var. *macrospema*: China; var. *jezoensis*: Hokkaido and Russia) along the eight regions. A: cone length (cm), B: cone width (cm), C: scale length (mm), D: scale width (mm).

the scatter diagram (Figures 3 and 4).

Individuals from Northern Korea, which was treated either var. *komarovii* or var. *koreana* (Uyeki, 1942; Fu *et al.*, 1999), could not be consistently distinguished from individuals from Russia and Northeastern China, which were usually referred as either var. *microsperma* or var. *jezoensis*. For example, cone length vs. width provided no separation of *P. jezoensis* sampled from Korea to China and no strong discontinuities existed among Northern individuals (Chinese and Russian individuals including Hokkaido individuals) in the diagram (Figure 3).

The frequency distribution of cone shape indicated that cone size variation among taxa fitted normal distribution (Figure 5). The P-P plot, which compared the empirical cumulative distribution function of a variable with a specified theoretical cumulative distribution function, also showed the linearity of the pattern (Figure 5). As a normality test, the Shapiro-Wilk test, which was more robust than other tests for skewness and kurtosis, showed *p*-value 0.068 for length and 0.338 for width. As

the computed *p*-value was greater than the significance level =0.05, we accepted the null hypothesis of normality. Therefore, morphological variation of these characters was deeply nested within this normal distribution, rejecting any recognition of taxonomic entity mainly based on cone morphology.

All measured characters appeared to show some clinal variation with changes in latitude, and a distinctive trend was evident in Figure 6. That is, as one considers a path from the south part of ranges to areas to the north, the cones of the *P. jezoensis* complex become larger in most respects and the largest cone size in northern Japan, Hokkaido.

In order to compare the variation within and among individuals, seven to nine cones from one individual tree were additionally compared with total data of each population (not shown). This analysis indicated that individual variation in terms of all characters generally resided within population variation, although a few data were evident outliers.

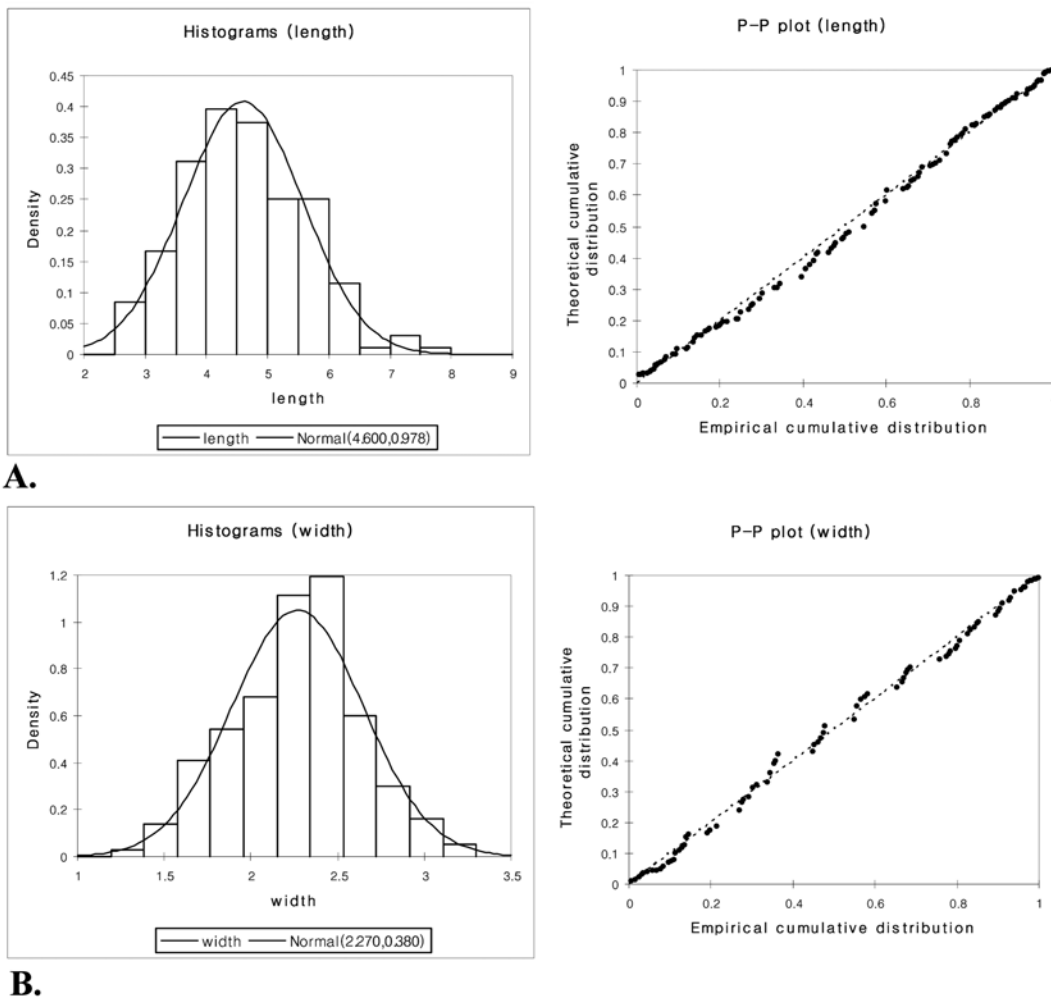


Figure 5. Histograms and P-P Plots of cone width and length. Curve lines have been drawn from normal distribution test. Both data show the normal distribution across the geographical range. A: cone length, B: cone width.

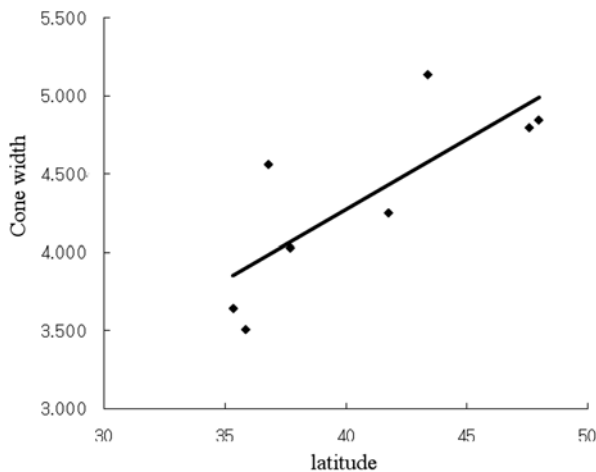


Figure 6. The mean values of cone width (unit: cm) from eight regions are plotted against the latitude (unit: degree). A geographical cline from south to north are well represented with *var. koreana*, *var. hondoensis*, and *var. jezoensis*.

Discussion

Jezo spruce is restricted to high elevations in the central region of Honshu Island of Japan, southern areas of Korean peninsula, the southern part of northeast China and the Far East of Russia (Kong and Watts, 1993; Yamazaki, 1995). Hence, these varieties of *P. jezoensis* might be divergent because of distribution-range expansion and isolation of the populations as a result of climate change during the Quaternary (Aizawa *et al.*, 2007). The nuclear SSR Marker (Aizawa *et al.*, 2007) and the allozyme data of *P. jezoensis* in Russia (Potenko and Knysh, 2003) supported the concept of the distribution change of the species in this region during the Quaternary.

Recent genetic study showed that populations in southern (Mt. Jiri-san of southern Korea) and northern (Kamchatka of the Far East of Russia) marginal populations had significantly less genetic diversity than those in central populations (Aizawa *et al.*, 2007). The more amount of genetic diversity was found in Hokkaido and the Far East of Russia followed by some populations of Honshu of Japan. The possible scenario for the present genetic occurrence was that these Hokkaido and other central populations might have served as sources for the colonization of regions. Some marginal populations could have been originated through dispersal. Genetic diversity and current population sizes indicated that Hokkaido and the Far East of Russian populations were substantially larger than today. Probably due to local extinctions and/or bottlenecks, this species might have been squeezed out of many areas and finally restricted to isolated stands at current marginal populations. Results of the current univariate analysis showed that all infraspecific taxa of

Picea jezoensis were not morphologically distinct with a major morphological continuum, which supported this scenario.

The data in Figures 3 and 4 supported that idea of a geographical cline from south to north with cone width and length. *Var. koreana* and *var. hondoensis* formed one end of cline along the south margins, while *var. jezoensis* formed another end of cline. Strandby *et al.* (2009) and Myers and Bormann (1963) demonstrated that several morphological characters of conifer taxa were correlated with altitude, latitude or longitude.

Aizawa *et al.* (2007) showed that the constructed networks of mitochondrial haplotypes of the centrally located populations in Asian continent, Sakhalin, and Hokkaido were different from those of the relative small size of geographically peripheral populations, such as Kamchatka, southern Korea, and Honshu populations of Japan. These results supported that stochasticity during Quaternary in eastern Asia had a large effect at such population margins. Therefore, the majority of the populations could be considered as one metapopulation with geographically marginal populations as possible outliers (*var. koreana* in Korea, *var. hondoensis* in central Japan, and *P. kamtschakensis* in the Far East of Russia). Substantial genetic impacts emerged at the marginal populations indicate that morphological variation is greatest across the ecological and geographical gradient, but the entities that comprise *P. jezoensis* exhibit widely overlapping ranges in all morphological attributes. Recent allozyme and isozyme study (Potenko, 2007a, 2007b) also rejected the taxonomic recognition of *P. ajanensis*, *P. microsperma*, and *P. komarovii* as distinctive taxa except *P. kamtschakensis*.

A consensus on the taxonomy of *Picea jezoensis* occurring in eastern Asia is undoubtedly still insufficient, but in our opinion a merger of currently accepted morphospecies is necessary. Consequently, cone data of the present study do not support continued recognition of the infraspecific taxa in eastern Asia. We suggest the following taxonomic treatment of the *P. jezoensis* complex here.

Taxonomic Treatment

1. *Picea jezoensis* (Siebold et Zucc.) Carrière

Traité Gén. Conif. 255 (1855) [Type: Lectotype, Japan, Jezo (=Hokkaido), Siebold, P.F. von *s.n.*, L 01133263!]

Abies jezoensis Siebold & Zucc., Fl. Jap. 2: 19, t. 110 (1842); *Pinus jezoensis* (Siebold. et Zucc.) Antoine, Conif. 97, t. 37, Figure 1 (1847); *Pinus firma* var. *jezoensis* Endlicher, Syn. Conif. 99 (1847); *Abies firma* var. *jezoensis* Carrière, Traité Gén. Conif. 212 (1855).

Abies ajanensis Lindl. & Gordon, J. Hort. Soc. London 5: 212 (1850) (type not seen); *Picea ajanensis* (Lindl. & Gor-

don) Fischer ex Carrière, *Traité Gén. Conif.* 259 (1855); *Tsuga ajanensis* Regel, *Russ. Dendr.* ed. 2, 39 (1883); *Picea jezoensis* var. *ajanensis* (Fisch. ex Carr.) W.C. Cheng et L.K. Fu, *Fl. Reipubl. Popularis Sin.* 7: 162 (1978).

Abies microsperma Lindl., *Gard. Chron.* 1861: 22 (1861) (type not seen); *Picea microsperma* (Lindley) Carrière, *Traité Gén. Conif.*, ed. 2, 339 (1867); *Picea ajanensis* var. *microsperma* (Lindley) Mast., *Gard. Chron. Ser.* 2, 13: 115 (1880); *Abies ajanensis* var. *microsperma* (Lindl.) Veitch, *Man. Conif.* 66 (1881); *Pinus jezoensis* f. *microsperma* (Mast.) Voss, Putlitz & Meyer, *Landlexikon* 4: 772 (1913).

Picea hondoensis Mayr, *Monogr. Abietin. Japan Reich.* 51, t. 4, Figure 9 (1890) (type not seen); *Pinus hondoensis* (Mayr) Voss, *Mitt. Deutsch. Dendrol. Ges.* 1907(16): 93 (1908); *Picea jezoensis* var. *hondoensis* (Mayr) Rehder, *Mitt. Deutsch. Dendrol. Ges.* 1915(24): 214 (1916); *Picea jezoensis* subsp. *hondoensis* (Mayr) P.A. Schmidt, *Haussknechtia* 4: 38 (1988).

Picea komarovii V. Vassil, *Bot. Zhurnm. (Moscow & Leningrad)* 35: 504 (1950) (type not seen); *Picea jezoensis* var. *komarovii* (V.Vassil) W.C. Cheng et L.K. Fu, *Fl. Reipubl. Popularis Sin.* 7: 161 (1978).

Picea jezoensis var. *koreana* Uyeki, *Bulletin of the Forest of Chosen (=Chosen Sanlin Kaihou)*, 206(7): 12 (1942) (type not seen).

Picea kamtschatskensis Lacass., *Bull. Soc. Hist. Nat. Toulouse*, 58: 637 (1929) (type not seen); *Picea jezoensis* (Siebold et Zucc.) Carrière f. *kamtschatskensis* (Lacass.) S.L. Tung et Y.L. Chou, *Ligneous Flora of Heilongjiang* 46 (1986).

Representative specimens examined: **Korea.** *Gangwon-do*: Hoiyang-gun, Naegeumgang-myeon, Mt. Geumgang-san, peak Mireukbong (=Prov. Kogen, Mt. Konggosan, Miroku-ho), 12 Oct. 1917, E.H. Wilson 9245 (A). *Gyeong-sangnam-do*: Hampyeong-gun, Mt. Jiri-san, Seseok, 30 July 1963, T.H. Cho, J.D. Park and T.B. Lee *s.n.* (SNUA); 28 July 1963, T.H. Cho, J.D. Park and T.B. Lee *s.n.* (SNUA); Sancheong-gun and Hamyang-gun, Macheon-myeon, Mt. Jiri-san, Peak Choenwangbong [Prov. S. Keisho, Mt. Chiri-san, Tenno-bo (=Tinnoboo)], 16 Nov. 1917, E.H. Wilson 9599 (A). *Hamgyeongbuk-do*: Musan-gun, Jucho (Prov. N. Kankyo, Jyosohyo), 19 Aug. 1917, E.H. Wilson 8964 (A). *Jeollabuk-do*: Mujugun, Mupung-myeon, Mt. Deokyu-san, from Guwuldam - temple Baekyeonsa - Peak Hyangjukbong, 1614 m alt., 13 Oct. 1995, J.-I. Jeon, C.-S. Chang 2428 (SNUA). *Jeollanam-do*: Gurye-gun, Mt. Jiri-san from Nogodan-Chunhwangbong, 29 June 1984, T.B. Lee *s.n.* (SNUA). **China.** *Heilongjiang Province*: Boli county, Hongqi forestry Center, 17 Sept. 1950, Y.L. Zhang 2154 (PE); Tangyuan County, 4 Oct. 1950, Liou, T.N. 1444 (PE); Tangyuan County and Sungkiang Sheong, 6 July 1950, T.N. Liou 1445 (PE); Songjiang District, 7 Oct. 1950,

Y.L. Zhang 447 (PE); *s.l., s.d.* 1959, L.R. Chen *s.n.* (PE). *Jiangsu Province*: Hongqi forestry Center, 810 m alt., *s.d.* C.Y. Wu 012 (PE). *Jilin Province*: Antu County, 1100 m alt. 8 Sept. 1951, T.N. Liou 4207 (PE); northern slope of Mt. Changbau Shan, 11 Aug. 1959, the first group of Yanbian 223 (PE); Fusong County, Man Jiang, no date, 1957, Y.L. Zhou 34 (PE); Fusong County, upper valley of Man Jiang, ca 121 m ESE Feng Ling Station, 1160-1250 m alt, 15 Aug. 1986, W.H. Sauer, S. Gerbert, T. Yang and D.-Y. Hong 33870 (PE); Fusong County, northern part of Mt. Changbai Shan, 1500 m alt. 11 Aug. 1959, Yanbian Exploration team 223 (PE); Fusong County, Mt. Changbai Shan, Tizihe, 21 July 1950, T.N. Liou and Z.Y. Wu 1478 (PE); Helonggou, 18 Sept. 1959, Yanbian Exploration team 977 (PE); Wangqing County, 13. Oct. 1955, G.Y. Li *s.n.* (PE); *s.l.*, 2 Aug. 1959, J. Sato 6545 (PE). **Japan Hokkaido**: Sapporo-shi, 24 Sept. 1889, Y. Momiyama 987 (MAK). *Nagano Prefecture*: Shimominochi-gun, Sakae-mura - Mt. Naebasan, 20 Aug. 1958, M. Mizushima *s.n.* (MAK). *Nara Prefecture*: Bukyogadake (=Hachikyogadake), 13 July 1915, G. Koidzumi *s.n.* (TI). *Tochigi Prefecture*: Nikko-shi, Gwangdeok, 1720 m alt. 12 Sept. 1993, M. Tsuchiya 6885 (MAK); Nikko-shi, Mt. Shirane, 29 Apr. 1913, G. Koidzumi *s.n.* (TI). *Tokyo Prefecture*: Nishitama-gun, Okutamamachi, Mt. Kumotori(-yama), 14 July 1935, K. Hiyama *s.n.* (MAK). **Russia Sakhalin Oblast**: Sakhalin Island, Approx. 8 km North of Dolinsk; Environs surrounding Nayba river near intersection with highway. N47° 24.640', E 142° 46.897', 23 July 2001, H. Takahashi 29298 (TI).

Distribution: Central Kamchatka, mainland Russia, the Far East of Russia (Sakhalin and south Kuril Inlands), northeastern and central China (Mt. Changbai), southern and central Japan (Hondo and Hokkaido), and Korea (Farjon, 1990; Yamazaki, 1995; Fu *et al.*, 1999).

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Appendix. Origin and accession number for specimens used for morphological analysis. Selected voucher specimens are deposited at T.B. Lee Herbarium of the Arboretum of Seoul National University (SNUA) or as otherwise indicated.

Japan: *Honshu:* Yumoto *s.n.* (A), E. H. Wilson 7860 (A), T. Yamazaki 6062 (A), E. H. Wilson 7520 (A), E. H. Wilson 7772 (A), E. H. Wilson 7647 (A), H. Muroi 3393 (A), Maximowicz *s.n.* (A), T. Yamazaki 6062 (A), M. Tsuchiya *s.n.*, 12 Sept. 1993 (MAK), T. Yano *s.n.*, 1 Aug. 1956 (MAK), M. Mizushima *s.n.*, 20 Aug. 1958 (MAK), Matsuyama, K. *s.n.*, 20 Aug. 1958 (MAK), K. Hiyama 6653 (MAK), S. Kobayashi *s.n.*, 25 Aug. 1960 (MAK), M. Hotta 11136., 5 Aug. 1962 (MAK, TI), T. Saito *s.n.*, 10 Sept. 1997 (MAK), T. Uakino *s.n.*, ? Nov. 1894 (TI), G. Koidzumi *s.n.*, 29 June 1913 (TI), G. Koidzumi *s.n.*, 13 July 1915 (TI), Y. Satake *s.n.*, 22 July 1933 (TI), J. Murata and H. Ohba 5120 (TI), H. Uematsu *s.n.*, *s.d.* 1985 (TI), G. Murata *s.n.*, 23 Aug. 1956 (TI), T. Yamazaki *s.n.*, 19 July 1944 (TI), D. Mayr *s.n.*, *s.d.* 1889 (TI), Unknown collector *s.n.*, 29 Aug. 1927 (TI), F. Maekawa *s.n.*, 11 Aug 1934 (TI), B. Hayata *s.n.*, 22 July 1924 (TI). *Hokkaido:* Wild collections (HK 050928-1, HK 050919-1, HK 050909-1, HK 050929-2, HK 050921-1, HK 050929-1, HK 050921-2, HK 050927-2, HK 050922-2, HK 050920-1, HK 050927-1, HK 050919-2, HK 050922-1, HK 050923-1), M. Takenouchi *s.n.*, *s.d.* (MAK), Y. Momiyama *s.n.*, 24 Sept. 1889 (TI), U. Faurie 6658 (A), S. Tsugaru 4872 (A), Y. Tokubuchi *s.n.* (A), Y. Tokubuchi *s.n.* (A), U. Faurie 6659 (A), G. Murata *et al.* 38421 (A), U. Faurie 8? (A), Koyama *et Fukuoka* 3530 (A), U. Faurie 6657 (A), Unknown (A), J. Mastumura *s.n.* (#1), 3 Aug. 1899 (TI), J. Mastumura *s.n.* (#2), 3 Aug. 1899 (TI), J. Mastumura *s.n.* (#3), 3 Aug. 1899 (TI), unknown collector *s.n.*, 25 June 1884 (TI), G. Murata *et al.* 38421 (TI), T. Yamazaki *s.n.*, 27 July 1985 (TI), G. Koidzumi *s.n.*, 17 Aug. 1916 (TI), T. S. Liu *s.n.*, 2 Aug. 1970 (TI),

M. Takahashi *s.n.*, ? June 1939 (TI), M. Takalas *s.n.*, ? Sept. 1937 (TI)

China: Maximowicz *s.n.*, *s.d.* 1855 (A), NACPEC97 (A), B. V. Skvortzov *s.n.* (A), B. W. Skvortzov *s.n.* (A), V. L. Komarov *s.n.* (A), Heilong Jiang wild collections (HJ 1, HJ 3, HJ 4, HJ 5, HJ 6, HJ 7, HJ 8, HJ 9, HJ 10, HJ 11, HJ 13, HJ 14, HJ 15, HJ 17, HJ 18, HJ 19, HJ 20, HJ 22, HJ 23, HJ 24), J. Sato 6545 (PE), Tong 3559 (PE), Liu 4207 (PE), Wu 012 (PE), Liu 875 (PE), Liu 1444 (PE), Liu 1445 (PE), Hao 16182 (PE), Zhang 2164 (PE), Zhu 129 (PE), Zhang 2154 (PE), Zhang 530 (PE), Zhou *s.n.* (PE), Zhang 1447 (PE), Zhang 1390 (PE), Zhou 34 (PE), Qian 427 (PE), Hong 33870 (PE), Liu 3535 (PE), Liu 4207 (PE), unknown collector 206 (PE), unknown collector *s.n.* (PE 1639596), unknown collector *s.n.* (PE 1639597), unknown collector 223 (PE), unknown collector 977 (PE), unknown collector 740 (PE), unknown collector 891 (PE)

Russia: wild collections (R 99, R 101, R 103, R 104, R 105, RA 1, RA 2, RA 3, RA 4), H. Takahashi 29298 (TI), S. Komatsu *s.n.* (#1) (TI), S. Komatsu *s.n.* (#2) (TI), S. Komatsu *s.n.* (#3) (TI), S. Komatsu *s.n.* (#4) (TI), Okada *s.n.* (TI), G. Nakahara *s.n.* (TI), S. Noshiro *et al.* *s.n.* (TI), S. Tsuji *et al.* *s.n.* (#1) (TI), S. Tsuji *et al.* *s.n.* (#2) (TI), T. Naito *s.n.* (TI), S. Seto 16193 (TI).

Korea: Jiri-san wild collections (JR 3, JR 4, JR 5, JR 6, JR 7, JR 8, JR 9, JR 10, JR 11, JR 12, JR 13, JR 14, JR 16, JR 17, JR 18, JR 20), Gyebang-san wild collections (GB 1, GB 2, GB 3, GB 4), Deokyu-san wild collections (DY 2, DY 9, DY 11), Chang 2068, Chang 2072, Chang 2065, Chang 2066, Chang 2074, Chang 2070, Chang 2076, Boratynski 325 (A), E.H. Wilson 8964 (A), E.H. Wilson 10452 (A), V.L. Komarov *s.n.* (A), E.H. Wilson 9148 (A), V.L. Komarov *s.n.*, 20 Aug. 20 1897 (A), E.H. Wilson 9599 (A).