Originals

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Geographic Variations of *Pinus parviflora* Needle Characteristics

Takashi SATO

Kamiichi High School, 444 Sainokamishin, Kamiichi, Toyama, 930-0424 JAPAN

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Geographic variations of *Pinus parviflora* were examined using needle size and anatomical traits. Needle samples from 43 populations ranging from Hokkaido to Kyushu were collected and classified according to 17 needle characteristics. Samples classified by the arrangement of resin ducts in a cross section of needle were quite variable, and no geographical groups had similar properties. Stoutness, serration, and the density of stomata correlated significantly with altitude. The stomata density and serration were also significantly associated with warmth index and annual mean temperature. No significant correlations were found between any needle characteristic and habitat latitude. Cluster analysis revealed three clusters, but these were not associated with geographic location.

Key words: geographic variation, needle anatomy, *Pinus parviflora*

The classification of trees under *Pinus parviflora* has been hotly debated for more than one hundred years. Siebold and Zuccarini (1842) first described the Japanese five-needle pine and named it *Pinus parviflora*. In 1890, Mayr proposed a new name, *Pinus pentaphylla*, for the subset of *P. parviflora* characterized by long cones, winged seeds and stout needles. Henry (1910) deemed *P. pentaphylla* a variety of *P. parviflora* and this view was supported by Ohwi (1953). Satake (1989), Vidakovic (1991), and Yamazaki (1995) further endorsed *P. parviflora* as a single species with two varieties.

Gaussen (1960) and de Férre (1966) suggested *P. parviflora* was closely related with the other Asian five-leaved pines. Mirov (1967) initially commented about the many taxonomic problems of the Strobi group of Eastern Asia. Recently, Farjon (1984), Krüssmann (1985) and Vidakovic (1991) also expressed concern for taxonomic problems involving *P. parviflora*. In this paper I will use the name "*P. parviflora*" to encompass both *P. parviflora* Siebold & Zucc. (1842) and *P. pentaphylla* Mayr (1890).

Koehne (1893), Hayata and Satake (1929), Doi and Morikawa (1929), Ishii (1938), de Férre (1966) and Kausik and Bhattacharya (1977) suggested that anatomical traits of needles were useful in classifying *Pinus*. This technique has been well demonstrated on other species. On the basis of the number and arrangement of resin ducts, the Siberian *P. pumila* was found to be more similar to the Hokkaido plants than to the Honshu plants (Sato 1993). Sato (1994) further divided *P. pumila* into three distinct types by the needle characteristics, i.e., the Siberia type, the Hokkaido type and the Honshu type.

The objective of this study was to analyze the geographic variations of needle characteristics among populations of *P. parviflora*, and to elucidate whether any geographical groups are recognized or not. The results of this analysis may provide basic understanding to discuss the taxonomic problem mentioned above.

Multivariate analysis has been used to clarify relationships among a species complex and to study geographical variation (Smouse and Saylor 1973a, 1973b, McCune 1988). This analysis has also proved useful in characterizing differences between predefined groups, particularly where hybridization may be involved (Mayer and Mesler 1993). Factor analysis as a kind of multivariate analysis has been used to understand geographic variation of *Pinus* (Piedra 1983). This multivariate analysis is a suitable method to analyze the geographic variation of *P. pumila* (Sato 1994) and to understand the relationships among *P. parviflora*, *P.* × *hakkodensis* and *P. pumila* in Mt. Tateyama, Japan (Sato 1995). Multivariate analysis was thus carried out on the needle characteristics.

Method

Forty-three populations (Table 1) of *P. parviflora* were chosen from the natural ranges in Japan based on the work of Hayashi (1960). More than ten trees, growing at least 2 m apart, were chosen in each population. One branchlet was sampled from a sunny crown of each tree, because Shimakura (1934) reported that needle stoutness differed between sunny and shade crowns.

A one-year-old fascicle was removed from each branchlet and the five needles were classified into several needle types according to the number and the arrangement of resin ducts referenced by Sato (1993). On one needle, the seventeen characteristics presented in Figure 1 were measured. The resulting descriptions and units are presented in Table 2.

Multivariate analysis, cluster analysis by Ward method, was carried out using the standardized data-set of average needle characteristics in each population.

Results

1. Variations of needle types

The needles examined were classified into ten needle types (Fig. 2), and the frequency of the needle type in the populations are shown in Fig. 3. The II-B needle type, with two resin ducts far from each other, was found in all populations. Populations consisted of the II-B type only were found in five localities, JOK, TKI, GOZ, RYU and HKO, ranging from 40°N to 33°N. Needle type III group, including III-E, III-M and III-S, was observed in 27 populations (63%) located in Hokkaido, Honshu and Kyushu. Needle type IV was found in two populations, OZA and HOU in Honshu. No distinct geographical grouping of the needle types was recognized.

2. Variation of needle characteristics

The mean sizes and average structural identifiers of needles in each population were calculated (Table 3). Needle length (NL) varied from 35 mm to 61 mm and averaged 47 mm. Significant positive relationships were found among NL, DR, DI and NR. The populations in middle latitudes had longer needles than those in higher or lower latitudes.

The mean values of LL and LA, indicating needle stoutness, were 739 μm and 883 μm, varying from 603 μm to 944 μm and from 726 μm to 1150 μm, respectively. The populations with stout needles longer than 1 mm in LA were AD2, AD3, MOP, DAI, SAM and HIK, and these populations were located in Central and Northern Honshu. The LL correlated significantly with LA, DE, DI and NST, and was inversely related to RR. The mean value of endodermis diameter (DE) was 290 μm (range 240 μm to 373 μm). Mean resin duct diameter (DR) was 83 μm (range 60 μm to 105 μm). DR positively correlated with NR and RDL. The populations with large resin ducts (>100 μm) were YUN, NAR, KUB, OZA and HOU. These

Table 1. Locations and environmental factors of investigated *Pinus parviflora* populations

Localities	Population code	Nearest meterological station	Latitude (°)	Altitude (m)	WI* (month·°C)	AMT** (°C)	Tree height (m)	Life form
<HOKKAIDO>								
Apoi, Hokkaido	AP3	Urakawa	42.1	200	52.4	6.8	5–15	erect
Uzuragawa, Hokkaido	UZU	Hakodate	42.0	500	51.1	5.9	5–15	erect
Esan, Hokkaido	ESA	Hakodate	41.8	420	51.6	6.0	1–4	ascending
Ekamiyama, Hokkaido	KMI	Hakodate	41.8	70	66.7	8.3	5–15	erect
<HONSHU>								
Jogakura, Aomori	JOK	Aomori	40.7	700	51.0	5.9	5–15	erect
Moriyoshiyama, Akita	MOR	Aomori	40.0	1000	49.7	5.6	5–15	erect
Kanshotaira, Yamagata	KAN	Akita	38.1	1410	38.5	4.4	5–15	erect
Komakusataira, Miyagi	KMA	Sendai	38.1	1080	49.3	6.2	4–8	erect
Adatarayama, Fukushima	AD2	Fukushima	37.6	1340	47.9	5.6	2–5	ascending
Adatarayama, Fukushima	AD3	Fukushima	37.6	960	61.6	7.7	5–12	erect
Jumanyama, Fukushima	JUM	Fukushima	37.5	448	75.7	10.3	5–15	erect
Oritate, Niigata	YUN	Niigata	37.3	350	89.4	11.3	10–15	erect
Okutadami, Fukushima	OKT	Niigata	37.2	800	69.6	8.8	10–15	erect
Naramata, Gunma	NAR	Maebashi	36.9	860	75.9	9.8	10–15	erect
Kubo, Gunma	KUB	Maebashi	36.8	650	85.1	10.9	10–15	erect
Motoshiranesan, Gunma	MOP	Nagano	36.6	2100	30.6	3.0	3–15	ascending
Happoone, Nagano	HAP	Nagano	36.6	1700	33.5	3.4	2–3	ascending
Daikandai, Toyama	DAI	Toyama	36.6	1620	36.4	3.8	5–15	erect
Shimonokotaira, Toyama	SHI	Toyama	36.6	1450	47.4	5.6	10–15	erect
Shirokimine, Toyama	SI1	Toyama	36.5	1580	43.2	4.9	2–4	ascending
Shirokimine, Toyama	SI2	Toyama	36.5	1320	51.7	6.3	10–15	erect
Ozanamigozenyama, Toyama	OZA	Toyama	36.5	650	75.4	9.7	10–15	erect
Arimine, Toyama	ARI	Toyama	36.4	1100	59.6	7.5	10–15	erect
Takanbo, Toyama	TAK	Toyama	36.4	520	84.3	10.7	10–15	erect
Sanpokuzureyama, Gifu	SAM	Takayama	36.3	1740	40.9	3.9	2–4	ascending
Ogimachi, Gifu	OGI	Takayama	36.3	540	79.4	10.5	10–15	erect
Hounzaki, Nagano	HOU	Matsumoto	36.2	1000	71.0	8.8	10–15	erect
Urushikakiuchi, Gifu	URU	Takayama	36.2	650	75.1	9.9	10–15	erect
Ueno, Gifu	UEN	Takayama	36.2	500	80.9	10.7	10–15	erect
Hikagetaira, Gifu	HIK	Takayama	36.1	1500	47.5	5.2	10–15	erect
Konashitaira, Gifu	KON	Takayama	36.1	1100	59.8	7.4	10–15	erect
Miboro, Gifu	MIB	Takayama	36.1	700	73.2	9.6	10–15	erect
Nishido, Gifu	NIS	Takayama	35.9	720	72.4	9.5	10–15	erect
Takigoshi, Nagano	TKI	Gifu	35.8	1100	59.8	7.4	10–15	erect
Asahi, Gifu	ASA	Gifu	35.7	400	84.8	11.3	10–15	erect
Gozaishoyama, Mie	GOZ	Tsu	35.0	960	75.6	9.8	5–15	erect
Ryugatake, Yamaguchi	RYU	Shimonoseki	34.3	450	97.0	12.5	5–15	erect
Koyasan, Nara	KOY	Nara	34.2	720	93.8	12.2	5–15	erect
Oosugidani, Mie	OOS	Tsu	34.2	380	101.5	13.0	5–15	erect
<SHIKOKU & KYUSHU>								
Higashikuromori, Kochi	HIG	Kochi	33.8	960	81.3	10.7	10–15	erect
Hikosan, Fukuoka	HKO	Fukuoka	33.5	640	98.0	12.7	5–15	erect
Kanosan, Ooita	KNO	Ooita	32.8	1548	47.0	6.3	5–15	erect
Ohira, Ooita	OHI	Ooita	32.8	540	98.4	12.8	5–15	erect

*: Kira's warmth index expected from the meteoric data observed in the nearest meteorological station.
**: annual mean temperature expected from the nearest meteorological station.

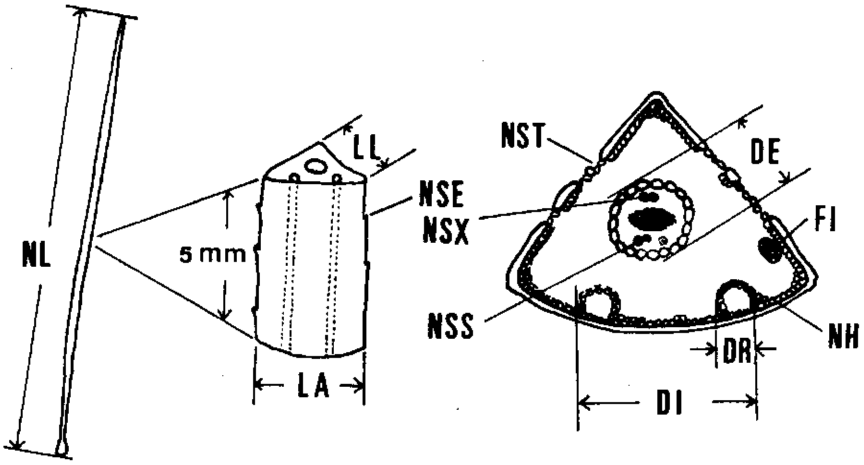

Fig. 1. Schematic drawing of a needle and its cross section, indicating sites of measurement for classifying characteristics. Characteristic codes are shown in Table 2.

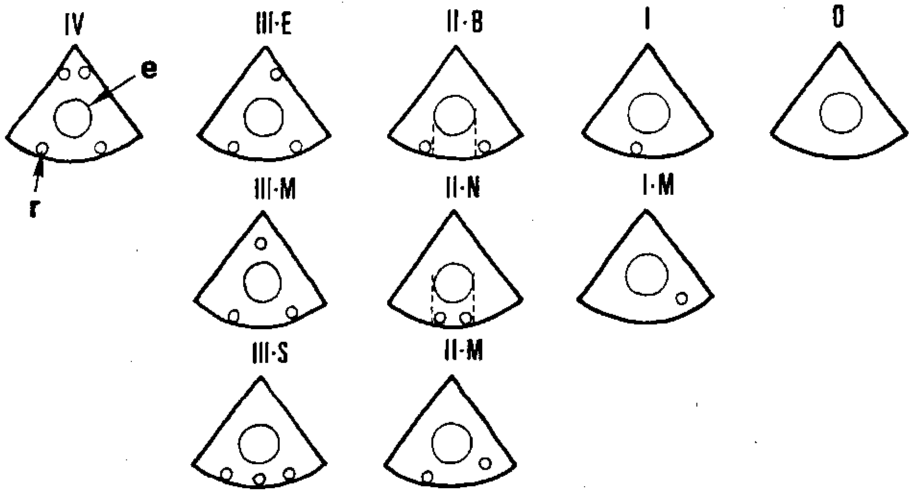

Fig. 2. Needle types classified by the arrangements of resin ducts. e: endodermis; r: resin duct. IV: 4 resin ducts, 2 external on the abaxial side and 2 external or middle in adaxial side. III-E: 3 resin ducts, 2 external on the abaxial side and 1 external on the adaxial side. III-M: 3 resin ducts, 2 external on the abaxial side and 1 centered in the adaxial side. III-S: 3 resin ducts, 3 external on the abaxial side. II-B: 2 resin ducts, with a separation wider than the diameter of the endoderm circle. II-N: 2 resin ducts, with a separation narrower than the diameter of the endoderm circle. II-M: 2 resin ducts, 1 external on the abaxial side and 1 centered in the abaxial. I: 1 resin duct, external on the abaxial side. I-M: 1 resin duct, centered in the abaxial side. 0: no resin duct.

Table 2. Needle characteristics of *Pinus parviflora*

Characteristic code*	Characteristics	Units or coding
NL	Needle length	mm
LL	Length of lateral side in cross section	μm
LA	Length of abaxial side in cross section	μm
DE	Diameter of the endoderm circle in cross section	μm
DR	Diameter of the largest resin duct in cross section	μm
DI	Distance between external resin ducts in cross section	μm
RE	Ratio DE/LL	ratio
RR	Ratio DR/LL	ratio
RD	Ratio DI/DE	ratio
RDL	Ratio DI/LA	ratio
NST	Number of stomata on a lateral side in cross section	n
NSE	Number of serrations on a central 5 mm of needle	n
FI	Number of idioblasts in mesophyll per section	n
NH	Number of hypoderm layers per abaxial side in cross section	n
NSX	Number of sclerenchyma cells in xylem side of transfusion tissue in cross section	n
NSS	Number of sclerenchyma cells in sieve side of transfusion tissue in cross section	n
NR	Number of resin ducts in cross section	n

*: see figure 2.

populations were located in the Mikuni and Hida Mountain ranges, Central Honshu. DI varied from 377 μm to 593 μm and averaged 460 μm.

The mean values of RE, RR, RD and RDL were 0.39, 0.11, 1.60 and 0.52 respectively. RR had a significant positive correlation with NR. RD had significant inverse correlations with NST and NSE. The mean number of stomata on a lateral face (NST) in each population was 3.7 and varied between 2.4 and 5.6. MOP, DAI and SAM had more than 5 stomata per lateral face. The mean number of lateral face serrations per central 5 mm (NSE) was 3.3 (range 2.0 to 6.0).

Mesophyll idioblasts were observed in eleven populations in Hokkaido and Honshu, but were not found in Shikoku or Kyushu. The number of idioblasts per section (FI) varied from 0 to 0.8 and averaged 0.1. The FI had significant positive correlation with NH. The mean value of NH in each population was almost 1. Hypoderm in all populations consisted of single cell layer with the exception of a few samples in the ASA population.

In all populations, sclerites in the xylem side of transfusion tissue (NSX) tended to number less than those on the sieve side (NSS). The mean values of NSX and NSS were 5.2 (2.8–9.5) and 7.7 (1.9–12.7), respectively. AD3, TAK, OGI and ASA, located in the Northern and Central Honshu, had an NSX>8 and an NSS>10. The NSX significantly correlated with NSS and NR.

The mean number of resin ducts in a cross section (NR) varied from 1.7 to 2.9 and averaged 2.1. The populations, OZA, TAK, HOU and HIK, located in Central Honshu, averaged more than 2.5 ducts per needle.

3. Differences of tree forms and areas

Most of the populations were consisted of erect trees but ascending trees were also observed on summits and steep ridges. Ascending trees were observed in ESA,

Table 3. Average needle characteristics in each population of *Pinus parviflora*

Population code	Sample sizes	Characteristics*																
		NL	LL	LA	DE	DR	DI	RE	RR	RD	RDL	NST	NSE	FI	NH	NSX	NSS	NR
<HOKKAIDO>																		
AP3	10	40	675	807	271	85	410	0.40	0.13	1.51	0.51	3.1	2.1	0.1	1.0	3.0	6.4	2.0
UZU	20	52	723	838	273	87	426	0.38	0.12	1.56	0.51	3.2	5.3	0.8	1.0	5.1	5.0	2.2
ESA	10	48	769	874	271	80	450	0.35	0.10	1.66	0.51	3.3	2.1	0.0	1.0	3.5	6.0	2.3
KMI	13	50	716	854	288	86	448	0.40	0.12	1.55	0.53	3.2	2.5	0.0	1.0	4.2	7.0	1.0
<HONSHU>																		
JOK	20	48	658	775	254	81	404	0.39	0.12	1.59	0.52	2.9	3.7	0.0	1.0	4.9	7.3	2.0
MOR	20	47	664	791	264	88	423	0.40	0.13	1.60	0.53	2.9	6.0	0.3	1.0	4.3	6.1	2.0
KAN	20	38	764	909	297	76	418	0.39	0.10	1.38	0.45	4.3	4.1	0.0	1.0	5.2	8.6	1.8
KMA	20	35	739	913	300	78	437	0.41	0.10	1.42	0.47	4.0	5.0	0.2	1.0	4.3	6.3	1.9
AD2	20	49	895	1053	373	81	517	0.42	0.09	1.37	0.48	4.7	4.3	0.0	1.0	4.9	7.5	1.9
AD3	20	46	845	1037	363	82	501	0.43	0.10	1.37	0.48	4.5	4.4	0.0	1.0	8.4	10.7	2.0
JUM	20	47	603	726	246	78	383	0.41	0.13	1.57	0.53	2.9	4.2	0.0	1.0	4.3	5.0	2.0
YUN	20	59	653	774	276	102	416	0.42	0.16	1.51	0.54	3.4	3.2	0.0	1.0	4.7	7.4	2.2
OKT	16	43	645	780	261	95	425	0.41	0.15	1.63	0.54	3.4	3.8	0.1	1.0	5.9	8.2	2.0
NAR	20	52	737	869	301	102	504	0.41	0.14	1.68	0.58	4.0	3.3	0.0	1.0	7.1	9.8	2.3
KUB	14	52	690	808	287	105	496	0.42	0.15	1.72	0.61	3.7	3.1	0.0	1.0	7.8	10.2	2.4
MOP	20	43	944	1150	362	85	593	0.38	0.09	1.65	0.51	5.5	4.5	0.0	1.0	5.6	7.1	2.0
HAP	10	41	755	944	301	86	407	0.40	0.11	1.34	0.43	4.1	2.0	0.1	1.0	3.6	7.3	1.9
DAI	21	52	931	1095	365	66	475	0.39	0.07	1.30	0.43	5.6	3.4	0.0	1.0	4.8	7.0	2.0
SHI	23	45	722	892	268	67	450	0.37	0.09	1.69	0.50	3.7	3.0	0.0	1.0	4.5	6.1	1.7
SI1	19	42	700	815	265	60	378	0.38	0.09	1.42	0.46	3.2	3.6	0.0	1.0	3.3	5.9	1.9
SI2	20	37	645	783	265	72	411	0.41	0.11	1.53	0.51	3.3	4.0	0.0	1.0	4.5	8.2	1.8
OZA	21	48	726	865	304	105	527	0.42	0.14	1.73	0.61	3.7	2.3	0.0	1.0	5.2	8.0	2.6
ARI	22	48	730	893	300	84	483	0.41	0.11	1.59	0.53	3.5	3.6	0.0	1.0	3.0	7.0	2.0
TAK	10	55	736	874	315	92	493	0.43	0.12	1.56	0.56	3.9	2.2	0.1	1.0	8.8	10.8	2.6
SAM	17	53	889	1034	351	97	450	0.40	0.11	1.28	0.43	5.2	4.4	0.0	1.0	5.4	12.7	1.9
OGI	10	50	719	869	286	85	469	0.40	0.12	1.64	0.54	3.3	3.1	0.2	1.0	8.9	10.4	2.2
HOU	20	48	799	930	316	101	479	0.40	0.13	1.51	0.51	3.8	3.7	0.0	1.0	6.8	7.8	2.9
URU	10	46	725	823	269	92	498	0.37	0.13	1.86	0.61	3.3	2.9	0.0	1.0	2.8	4.9	2.2
UEN	11	51	691	847	281	85	519	0.41	0.12	1.83	0.60	2.7	2.3	0.0	1.0	5.3	8.5	1.7
HIK	11	54	893	1049	318	98	562	0.36	0.11	1.77	0.54	4.7	3.5	0.0	1.0	7.9	9.5	2.5
KON	10	55	730	860	291	87	502	0.40	0.12	1.72	0.58	3.1	3.0	0.1	1.0	4.1	8.5	2.0
MIB	10	47	741	868	280	78	479	0.38	0.11	1.72	0.55	3.5	2.2	0.0	1.0	5.4	7.8	2.4
NIS	9	61	697	814	261	87	468	0.38	0.13	1.79	0.57	3.1	2.2	0.2	1.0	4.9	6.4	2.3
TKI	20	45	648	813	246	69	429	0.38	0.11	1.74	0.53	2.9	3.5	0.0	1.0	5.5	6.3	2.0
ASA	11	51	732	898	301	91	492	0.41	0.12	1.64	0.55	3.2	3.0	0.7	1.1	9.5	11.1	2.4
GOZ	11	38	746	868	287	91	453	0.39	0.12	1.58	0.52	4.2	2.9	0.0	1.0	4.3	6.4	2.0
RYU	10	37	677	791	240	62	377	0.35	0.09	1.57	0.48	2.4	2.5	0.0	1.0	4.5	7.3	2.0
KOY	20	51	720	895	312	74	483	0.44	0.10	1.54	0.54	3.6	3.2	0.0	1.0	4.9	7.1	1.9
COS	11	43	683	813	250	65	401	0.37	0.10	1.61	0.50	2.6	2.3	0.0	1.0	4.5	6.5	2.0
<SHIKOKU & KYUSHU>																		
HIG	18	38	756	910	277	71	470	0.37	0.09	1.71	0.52	3.7	2.4	0.0	1.0	5.5	9.2	1.9
HKO	20	40	756	929	272	70	449	0.36	0.09	1.65	0.48	4.1	2.1	0.0	1.0	3.0	7.5	2.0
KNO	20	41	774	924	271	77	436	0.35	0.10	1.69	0.50	4.3	4.4	0.0	1.0	4.6	5.8	2.0
OHI	20	49	758	894	275	71	493	0.36	0.09	1.79	0.55	3.7	2.3	0.0	1.0	3.7	6.9	2.0
mean		47	739	883	290	83	460	0.39	0.11	1.60	0.52	3.7	3.3	0.1	1.0	5.2	7.7	2.1
SE		1	12	14	5	2	7	0.00	0.00	0.02	0.01	0.1	0.1	0.0	0.0	0.3	0.3	0.0
Maximum		61	944	1150	373	105	593	0.44	0.16	1.86	0.61	5.6	6.0	0.8	1.1	9.5	12.7	2.9
Minimum		35	603	726	240	60	377	0.35	0.07	1.28	0.43	2.4	2.0	0.0	1.0	2.8	4.9	1.7

*: see Table 2 and Fig. 1.

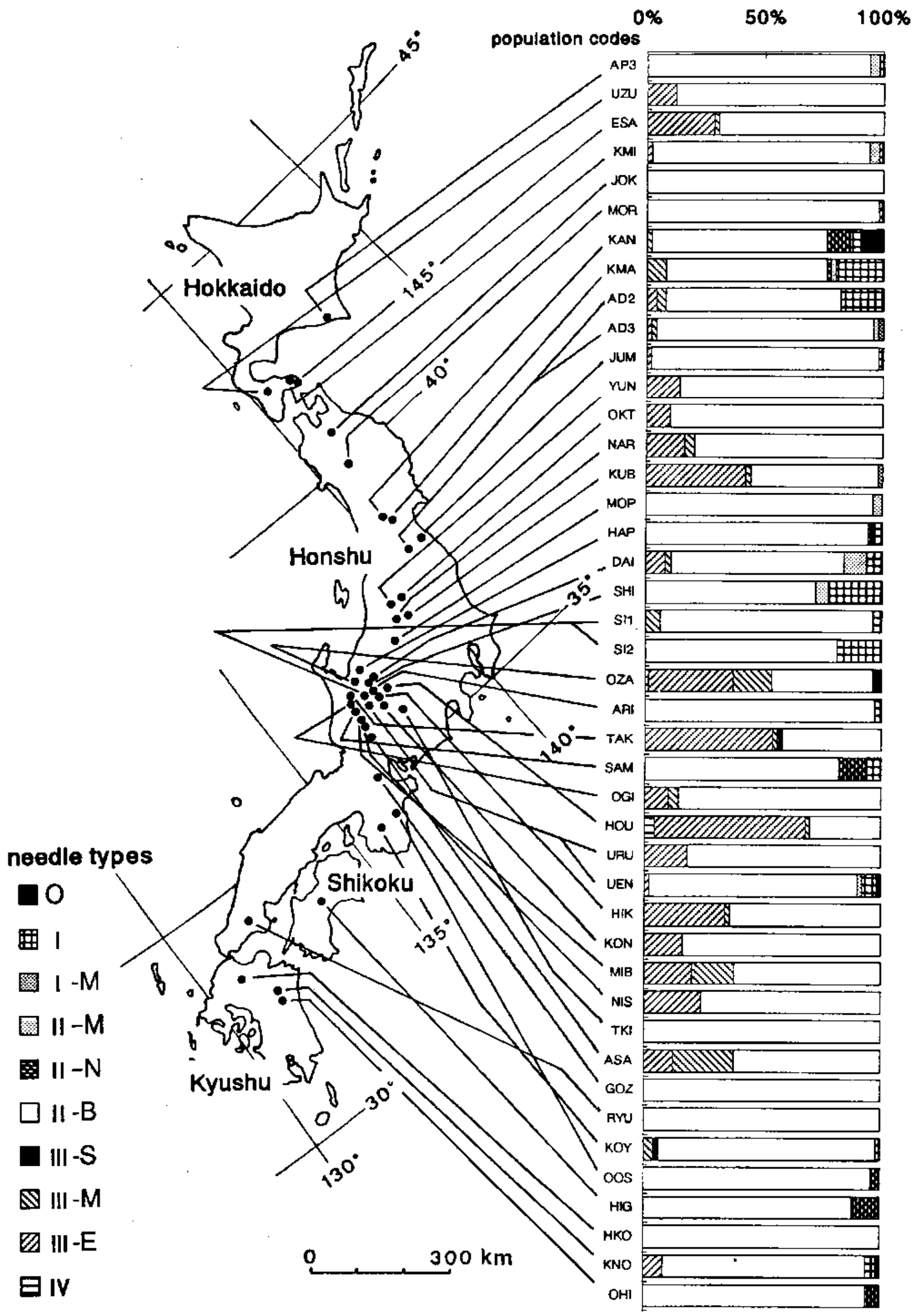

Fig. 3. Population codes and the frequencies of needle type in each population in *Pinus parviflora*. Needle types are shown in Fig. 2.

AD2, MOP, HAP, SI1 and SAM. The average needle characteristics of erect and ascending trees were compared. Significant differences were observed in the value of LL, LA, RD and RDL between the two groups (Table 4). The mean values of LL and LA in ascending trees were larger than those in erect trees. Mean values of RD and RDL were comparatively smaller in the ascending group. This may have been caused by a slight difference in DI between the two population groups, despite higher averages of LA and DE in ascending trees.

ANOVA results of the three areas, Hokkaido, Honshu, and Shikoku and Kyushu are shown in Table 4. The only significant difference among the three areas was in RE, with Honshu trees averaging larger REs.

4. Correlations between needle characteristics and geographic or climatic factors

There were no significant correlations between habitat latitude and needle characteristics. Eight characteristics, LL, LA, DE, RR, RD, RDL, NST and NSE, correlated significantly with altitude (Table 5). LL, LA, DE, NST and NSE, had positive correlations with altitude. Adaptation to the intense environments of summits or steep ridges may be responsible for increased needle thickness (LL, LA), endodermis circle diameter (DE), serration (NSE) and numbers of stomata (NST). Three characteristics, RR, RD and RDL, correlated inversely with altitude. Resin duct size and arrangement are more plastic as DR and DI show small variances.

Only RDL, NST, and NSE showed significant associations with climatic factors. RDL had significant positive correlation with the Kira's warmth index (WI) and annual mean temperature (AMT) of habitats. The distance between resin ducts becomes larger with warmer temperatures. The NST and NSE correlated inversely with WI and AMT.

Table 4. Average needle characteristics in each population group divided by life form and area in *Pinus parviflora*

	Life form											
	Erect (n=37)		Ascending (n=6)		t-test	<HOKKAIDO> (n=4)		<HONSHU> (n−35)		<SHIKOKU & KYUSHU> (n=4)		Result of ANOVA
Characteristics*	Mean	CL	Mean	CL	t value	mean	CL	mean	CL	mean	CL	F value
NL	47	2	46	4	0.48	47	5	47	2	42	5	1.32
LL	726	22	825	79	3.23**	721	38	739	29	761	9	0.26
LA	867	26	978	101	2.99**	843	28	883	34	914	16	0.59
DE	285	9	320	39	2.61	276	8	293	12	274	3	0.99
DR	83	4	82	10	0.35	84	3	84	4	72	3	1.98
DI	459	14	466	64	0.31	434	19	463	17	462	25	0.65
RE	0.39	0.01	0.39	0.02	0.62	0.38	0.02	0.40	0.01	0.36	0.01	6.19**
RR	0.12	0.01	0.10	0.01	2.11	0.12	0.01	0.12	0.01	0.10	0.00	2.20
RD	1.62	0.04	1.45	0.13	2.83**	1.57	0.06	1.58	0.05	1.71	0.06	1.47
RDL	0.53	0.01	0.47	0.03	3.20**	0.51	0.01	0.52	0.02	0.51	0.03	0.14
NST	3.5	0.2	4.3	0.8	2.63	3.2	0.1	3.7	0.3	3.9	0.3	1.02
NSE	3.3	0.3	3.5	0.9	0.49	3.0	1.5	3.4	0.3	2.8	1.1	0.84
FI	0.1	0.1	0.0	0.0	0.77	0.2	0.4	0.1	0.0	0.0	0.0	2.21
NH	1.0	0.0	1.0	0.0	0.50	1.0	0.0	1.0	0.0	1.0	0.0	1.34
NSX	5.3	0.6	4.4	0.9	1.26	4.0	0.9	5.4	0.6	4.2	1.1	2.25
NSS	7.6	0.5	7.7	2.1	0.13	6.1	0.8	7.9	0.6	7.3	1.4	1.93
NR	2.1	0.1	2.0	0.1	0.89	2.1	0.2	2.1	0.1	2.0	0.1	0.45

CL: confidence limit of mean value.
*: see Table 2 and Fig. 1.
**: shows significant at 1 % level.

Table 5. Correlation coefficients among needle characteristics and environmental factors of habitats in *Pinus parviflora*

Needle characteristics*	Geographic factors		Climatic factors**	
	Latitude	Altitude	WI	AMT
NL	0.112	−0.237	0.166	0.140
LL	−0.123	**0.603**	−0.429	−0.454
LA	−0.170	**0.644**	−0.431	−0.451
DE	−0.005	0.478	−0.361	−0.383
DR	0.241	−0.155	0.042	0.033
DI	−0.193	0.189	0.012	0.011
RE	0.223	−0.164	0.072	0.074
RR	0.284	**−0.487**	0.286	0.294
RD	−0.257	−0.346	0.448	0.476
RDL	−0.055	**−0.517**	**0.510**	**0.535**
NST	−0.149	**0.701**	**−0.478**	**−0.496**
NSE	0.264	0.411	**−0.509**	**−0.509**
FI	0.290	−0.233	−0.023	−0.015
NH	−0.140	−0.120	0.174	0.177
NSX	−0.092	−0.066	0.164	0.158
NSS	−0.177	0.072	0.126	0.099
NR	0.016	−0.271	0.260	0.248

Boldface value shows significance correlation ($P < 0.01$).

*: see Table 2 and Fig. 1.

**: see Table 1.

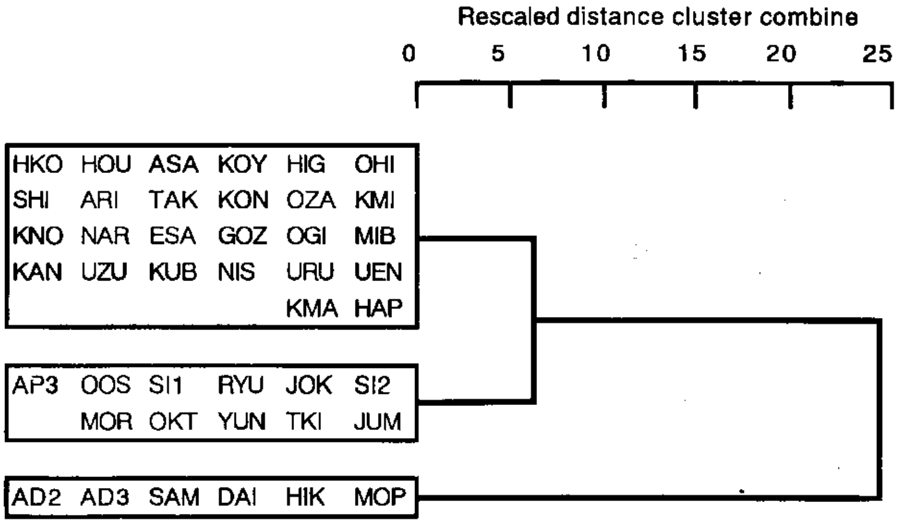

Fig. 4. Dendrogram drawn by the result of cluster analysis of the 17 needle characteristics in *Pinus parviflora*. Populations are shown by the population codes in Table 1.

5. Multivariate analysis

Cluster analysis result, using Ward method, is shown in Fig. 4. Three large clusters were identified. The first cluster included 26 populations scattered throughout Hokkaido, Honshu and Shikoku. The second cluster consisted of 11 populations in Hokkaido and Honshu. The third cluster included six populations in Central and Northern Honshu. The locations of these populations were shown in Fig. 5. There was no geographic gathering in each cluster of populations.

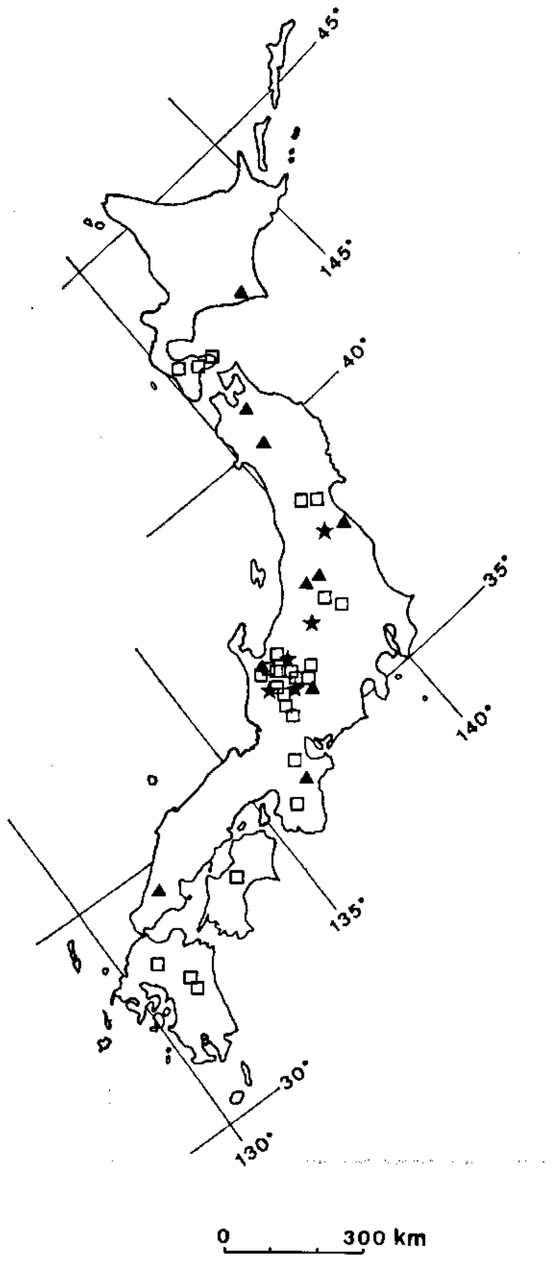

Fig. 5. The distribution of populations defined by cluster analysis in *Pinus parviflora*. □: cluster 1; ▲: cluster 2; ★:cluster 3.

Discussion

Needle type did not correlate with geographic divisions. Populations with greater needle diversity were located in Central Japan. I expected to see a topocline in needle characteristics, as Mergen (1963) reported a decrease in needle length and number of stomata and an increase in number of resin ducts with increasing latitude in *P. strobus* in North America. In my study, however, there was no significant correlation between any characteristics and habitat latitude. Indices for stoutness (LL, LA), number of stomata (NST), and serration (NSE) were significantly correlated with habitat altitude. These characteristics were most likely affected by altitude-related environmental factors, especially temperature and wind force. The stomata densities of many alpine plants in Alps exhibit increases with elevation (Körner et al. 1989). Castrillo (1995) reported alpine plants had a tendency to increase maximum rates of photosynthesis with elevation. Rundel and Yoder (1998) reported *Pinus cembra* growing on higher elevations were attributed to adaptation for high wind speed, low temperature and desiccation by making the cluster of needles pressed closely together. It reduces stomatal transpiration in low light intensity. But when light intensity strengthens, the cluster of needles opens and transpiration increases with many stomata to lead to high maximum rates of photosynthesis. These altitudinal change of stomata density such as NST may account for adaptation to severe environments.

Ascending trees, mostly found at higher

altitudes, had stouter needles than the populations of erect trees. This suggests that adaptations of tree form to summits or higher altitudes are paralleled by needle stoutness. Hayashi (1960) suggested that needle stoutness was a key characteristic to distinguish Southern and Northern types of *P. parviflora*. My results contradict this, indicating that stouter needles are predictors of altitude, not latitude, and are thus unsuitable for classifying this species into Southern and Northern types.

In *Pinus cembra*, mean needle length shortens by about 30% in elevation from 1300 to 2000 m in Austria Alps (Tranquillini 1965). In *P. parviflora*, the needle length (NL) had no significant correlation's with altitude, although both species ranges up to timberline. It is likely that *P. parviflora* adapts to severe environment in higher elevation by stoutness of needle differing from *P. cembra* shortens length of needle.

Multivariate analysis of needle characteristics identified three population clusters of *P. parviflora*. However, the clusters overlapped geographically and could not define distinct zones of tree type. Differences in needle characteristics were presumable indicators of local topography and environmental factors such as temperature and wind force. No needle characteristics were acceptable indicators for geographic distinction of tree type. By the result of analysis on the geographic variation of needle characteristics it is suggested that *P. parviflora* includes no distinct intraspecific taxon.

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佐藤　卓：ゴヨウマツに見られる針葉の地理的変異

ゴヨウマツの針葉のサイズと解剖学的性質の地理的な変異を調べた．ゴヨウマツの分布域を網羅する43個体群から，針葉を採取し，針葉長（NL）や鋸歯密度（NSE），樹脂道の直径（DR）など17形質と針葉タイプを観察した．針葉タイプは針葉横断面に見られる樹脂道の数と分布から，10タイプに分けられた．個体群ごとの針葉タイプの割合は変異が大きく，地理的なまとまりや傾向は見られなかった．北海道，本州，四国九州の3地域に分けた場合，地域間に有意差が認められた形質は維管束鞘直径と針葉横断面の側辺長の比（RE）だけであった．産地の緯度と17の針葉形質の間に有意な相関関係は見られなかった．産地の標高と，針葉横断面の側辺長（LL），背軸側辺長（LA），気孔密度（NST）は正の相関が，樹脂道直径比（RR）と樹脂道間隔比（RDL）は負の相関がそれぞれ認められた．産地のWIや年平均気温と有意な相関が認められた形質は，樹脂道間隔比（RDL），気孔密度（NST），鋸歯密度（NSE）であった．針葉の17形質を用いてクラスター分析をした結果，大きく3つのクラスターが区別された．しかし，それぞれのクラスターに属する個体群の分布は重なっており，顕著な地域的なまとまりは見られなかった．

（富山県立上市高等学校）