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Provenance tests for survival and growth of 50-year-old Japanese larch (*Larix kaempferi*) trees related to climatic conditions in central Japan

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Abstract Survival and growth of Japanese larch (*Larix kaempferi*) from 25 provenances in the natural distributional range were examined at three test sites in central Japan. Climatic conditions of the sites and provenances indicated a contrast between northwest and southeast locations across the distributional range. Density, height, diameter, and crookedness of stems and width and length of branches were measured for 50-year-old trees, and per-area cross-sectional area and volume of stems were calculated. Variance components among the provenances were large in the stem area and volume (27–33 %) and the branch width (26 %); those among the sites were large in the stem height, diameter, and density (70–81 %); and those of interaction between sites and provenances were small (0–12 %) in all the variables. Principal component analyses showed that eastern provenances exhibited large size of stems and branches at most sites. Growth rate and maximum size at each site were estimated from fitting the stem volume at three ages (12, 31 or 32, and 50 years) to growth curves in logistic functions. Eastern provenances, where seasonal variation is least in temperature and most in precipitation, showed the highest performance of stem and branch growth. The findings from our long-term survey of the *L. kaempferi* provenance tests suggest climatic effects on survival and growth traits and potential provenances from which to select new breeding materials.

Keywords Growth curve · Logistic function · Principal component analysis · Stem volume · Variance component

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Introduction

Japanese larch (*Larix kaempferi*) is one of the major plantation species in northern and central regions of Japan (Kurinobu 2005). This species has been introduced mainly in Europe, northern China, and North America and sometimes outgrows indigenous larches (Park and Fowler 1983; Paques 1996). The natural habitats of *L. kaempferi* are limited to the mountain range in the central part of the Japanese mainland, and this species was introduced to Hokkaido, the northernmost part of Japan (Fig. 1). This species is distributed in the lowest latitude among Eurasian larches and most diverged in nuclear and organeller genomes (Khatab et al. 2008; Polezhaeva et al. 2010). Maternally inherited mitochondrial DNA variation displayed geographic structure within *L. kaempferi* despite the restricted natural distribution (San Jose-Maldia et al. 2009). Thus, trait variation among provenances is expected in *L. kaempferi* because of its fragmented habitats and heterogeneous environments in the mountain range and different climates between the opposite coastal sides of the Japanese mainland.

Rapid juvenile growth and coarser branching are merits of *L. kaempferi* as compared with European larch (*L. decidua*) (Paques 2004) and American tamarack (*L. laricina*) (Park and Fowler 1983). In Japan, 530 plus trees of *L. kaempferi* had been selected and used in clonal seed orchards to produce improved seeds (Kurinobu 2005). The superiority of the plus trees in juvenile stem growth over commercial seed sources and the significant variation among families of the plus trees

Fig. 1 Map of provenances and test sites for *Larix kaempferi* in central Japan. *Open* and *closed symbols* show provenances and test sites, respectively. *Different shapes of symbols* indicate different regions in Table 1. *Gray areas* indicate natural habitats
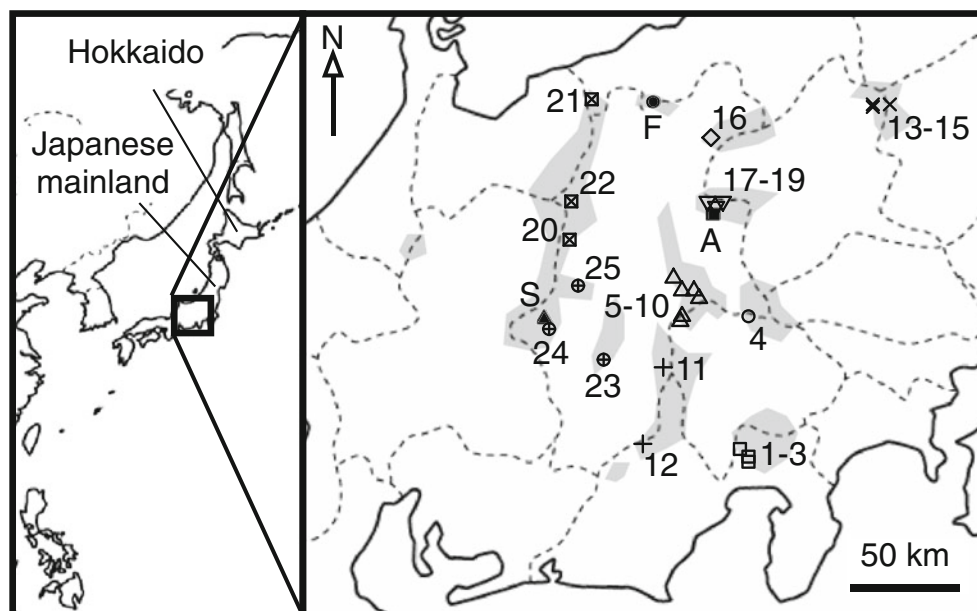
were confirmed by open-pollinated progeny tests (Kurinobu 2005). Genotype–environment interactions in the stem growth detected by the progeny tests were sometimes not neglectable, suggesting that matching between provenances and plantation sites is effective for maximizing genetic gain (Kurinobu 2005). In addition to the stem growth, branch traits and crown forms have been considered in the breeding of *L. kaempferi* (Toda and Mikami 1976).

Growth curves expressed in various mathematical functions are useful to predict the stem size at certain ages and to characterize growth patterns in various combinations between fast or slow growth and small or large maximum size. Growth curves were fit to the stem heights of 7- to 29-year-old *L. kaempferi* trees planted in Canada, and variation in the growth rate was found among provenances (Magnussen and Park 1991). For estimating the growth of organisms, a general function was proposed (Richards 1959), and some specific functions, such as Mitscherlich and logistic functions, are derived from the general function. These functions have been applied to the stem growth in tree plantations (Ito 1988).

An international program of provenance studies on *L. kaempferi* was planned in 1955, and test sites were established in Japan, Europe, and North America (Toda and Mikami 1976). At a test site in France, traits of stems, branches, and wood of trees that originated from 12 Japanese provenances were measured at 36 years of age (Paques 1996). At a test site in Canada, the stem height and diameter of trees from 20 provenances were measured at 4 to 19 years of age (Park and Fowler 1983). These provenance tests showed variation in the traits among the provenances, but geographic properties such as longitude, latitude, and altitude and climatic features such as temperature and precipitation in the provenances were not related to the stem size (Park and Fowler 1983; Paques 1996). At four test sites in

Japan, stem and branch traits of trees from 25 provenances were measured at two ages, 9 and 31 or 32 years (Toda and Mikami 1976; Nagasaka et al. 2011). These provenance tests showed variation in the stem and branch traits among the provenances and similar traits in neighboring provenances, suggesting that the trait variation depends on geographic patterns in the environmental and climatic conditions. Recently, we obtained measurements at 50 years of age at three of the four sites, which enable us to evaluate traits at logging ages and survival and growth during 50 years. Such long-term surveys of provenance tests are rare, and the knowledge obtained from such tests is valuable for the breeding of *L. kaempferi*.

In this study, we investigated survival and growth in *L. kaempferi* trees from the 25 provenances at the three sites. First, climatic conditions of the sites and provenances were examined. Second, we examined stem and branch traits in 50-year-old trees and evaluated their variance components among the sites, provenances, and interactions between them. We also performed principal component analyses to find provenances with high performance in the traits. Third, we fit growth curves to stem volume at 12 to 50 years of ages to characterize growth patterns of the provenances. Finally, we evaluated the relationship between the climatic conditions and the provenance traits.

Materials and methods

Design of tests

Across the natural distributional range of *L. kaempferi* (Lamb.) Carrière (Pinaceae), 25 provenances were selected from nine regions and coded as the Schmalenbeck numbers (Toda and Mikami 1976) (Table 1, Fig. 1). For each

Table 1 Location of provenances, from which *Larix kaempferi* seeds were collected, stem cross-sectional area at breast height (*A*), and stem-volume index (*V*) per planted area for provenances averaged over test sites

Sch. no.	Region	Locality	Longitude (°E)	Latitude (°N)	Altitude (m)	A (m^2 ha^{-1})	V (m^3 ha^{-1})
1	Fujisan	Tenzin pass	138.67	35.43	1,320	48.4	1,158
2	Fujisan	Sangoome	138.72	35.40	1,760	47.8	1,096
3	Fujisan	Oniwa	138.72	35.38	2,425	52.4	1,236
4	Kobushi-dake	Kobushi-dake	138.72	35.95	1,500	41.6	975
5	Yatsugatake	Inago	138.40	36.05	1,775	35.6	841
6	Yatsugatake	Uminokuchi	138.43	36.02	1,750	39.2	924
7	Yatsugatake	Tadeshina	138.28	36.10	1,600	38.9	890
8	Yatsugatake	Toyohira	138.33	36.05	1,700	40.7	918
9	Yatsugatake	Lower Tatsusawa	138.32	35.93	1,450	41.4	952
10	Yatsugatake	Upper Tatsusawa	138.33	35.95	1,750	40.7	953
11	Minami Alps	Kai Komagatake	138.22	35.75	1,500	33.6	776
12	Minami Alps	Akaishi Ohsawa-dake	138.10	35.45	2,000	28.9	628
13	Nikko	Akanuma	139.45	36.77	1,360	40.4	934
14	Nikko	Kohtoku	139.45	36.78	1,490	40.8	921
15	Nikko	Yashubara	139.55	36.78	1,700	44.4	1001
16	Kusatsu	Manza	138.50	36.65	1,750	38.0	887
17	Asama-yama	Lower Mizunoto	138.48	36.40	1,900	34.0	764
18	Asama-yama	Kutsukake	138.57	36.40	1,425	35.2	753
19	Asama-yama	Oiwake	138.53	36.38	1,700	29.1	605
20	Kita Alps	Kamikohchi	137.67	36.25	1,620	37.9	860
21	Kita Alps	Renge-dake	137.80	36.80	2,180	26.7[a]	584[a]
22	Kita Alps	Lower Takasegawa valley	137.68	36.40	1,380	33.8	752
23	Kiso	Kiso Komagatake	137.87	35.78	1,800	34.0	790
24	Kiso	Ontake	137.55	35.90	1,380	38.9	881
25	Kiso	Hachimori-yama	137.72	36.07	1,920	37.7	847

[a] Values were obtained from Asama because trees from provenance Renge-dake are absent in Fujisato and Shintaka

provenance, seeds were collected in 1956 from approximately 20 maternal trees, of which mean height ranged from 3.6 to 27.2 m and mean diameter at breast height (DBH) ranged from 22.2 to 79.4 cm (Toda and Mikami 1976; Nagasaka et al. 2011). The seeds from each provenance were mixed among families and raised to seedlings.

Three test sites, named as Asama, Fujisato, and Shintaka, were established in central Japan (Table 2, Fig. 1). The sites were divided into multiple plots in various spatial arrangements, and the plots were assigned to provenances randomly or systematically (Appendix 1). In Asama, 144 seedlings from each of the 25 provenances were planted at each of 100 plots (21.6×21.6 m, four replicates for each provenance) in April 1959. In Fujisato, 84 seedlings from each of 24 provenances except for Renge-dake (Sch. 21) were planted at each of 96 plots (12.6×21.6 m, four replicates) in April 1959. In Shintaka, 84 seedlings from each of the 24 provenances were planted at each of 72 plots (12.6×21.6 m, three replicates) in November 1958. The seedlings were planted at intervals of 1.8 m in both rows and columns within plots. In 1971, the 12-year-old trees were thinned by half in zigzag patterns.

Climatic conditions

Climatic conditions are expected to affect traits of the provenances and performance at the test sites. Thus, we obtained 19 bio-climatic variables (BIO1-19) of the three sites and the 25 provenances at a resolution of 1 min from WorldClim (Hijmans et al. 2005). To summarize climatic conditions, we performed a principal component analysis for the sites and provenances with the standardized variables using function princomp in statistical environment R 2.15.1 (R Development Core Team 2012). Because some variables were highly correlated with each other, we removed some redundant variables from the analysis. We characterized climatic conditions of the sites and provenances in the nine regions according to the first and second principal components and loading of the examined variables on the components.

Measurement

In 2009, when the planted trees were 50 years old, we censussed the number of living stems, measured height

Table 2 Properties of test sites, where *Larix kaempferi* trees were planted, and measures of stem and branch traits and stem mass per planted area in 50-year-old trees except for those from provenance Renge-dake (Sch. 21; Table 1), which are absent in Fujisato and Shintaka

	Test site		
Property	Asama	Fujisato	Shintaka
Region	Asamayama	Kita Alps	Kiso
Longitude (°E)	138.51	138.16	137.52
Latitude (°N)	36.35	36.79	35.94
Altitude (m)	1,000	900	1,650
Direction of slope	SW	NE	SSE
Angle (°) of slope	3	9	20
Variable	Asama	Fujisato	Shintaka
Stem height (m)	24.76	23.58	19.34
Stem diameter (cm) at breast height	30.36	25.71	22.54
Stem density (ha^{-1})	520.74	758.21	1,015.03
Per-area stem cross-sectional area (m^2 ha^{-1}) at breast height	37.06	39.36	40.72
Per-area stem volume index (m^3 ha^{-1})	924.64	934.57	790.75
Branch width (score: 1–3)	2.16	1.97	1.84
Branch length (score: 1–3)	1.96	1.65	1.81
Stem crookedness (score: 1–3)	1.71	1.47	1.36

(H, m) and DBH (cm) of the stems, and recorded width and length of branches and crookedness of the stems in three (1, 2, and 3) scores for 25.0±5.7 (mean ± SD, ranging from 5 to 38) trees at each plot. Density (D, ha^{-1}) of the stems was calculated from the number of the stems and the area where the trees were planted. Cross-sectional area (A, m^2 ha^{-1}) of the stems at breast height per area was obtained from $A = \pi d^2 D/200^2$, where d is the mean DBH. Stem-volume index per area (V, m^3 ha^{-1}) was obtained from $V = Ah$ for the trees, where h is mean H. In Asama, six plots for provenances Sch. 7, 9, 11, 12, 18, and 24 and two plots for Sch. 13 were damaged due to a forest fire in 1983 (Appendix 1). Measures at the eight damaged plots were not available.

In 1990 (32 years of age) in Asama, and in 1989 (31 years of age) in Fujisato and Shintaka, the number, height (m), and DBH (cm) of stems were measured in the same way (Nagasaka et al. 2011). In 1968 (9 years of age), 3 years before the thinning, the stem height and diameter were also measured at the three sites (Toda and Mikami 1976). However, 32-year-old trees at a plot for provenance Sch. 1 in Asama and 31- and 9-year-old trees at 24 plots for all the provenances (one of the four replicates) in Fujisato were not measured. From these measures and the planted area, we calculated the per-area stem-volume index (m^3 ha^{-1}) in the same way. We obtained the index at 12 years of age, when the thinning had just been finnished, from the number of remaining stems after the thinning and the mean stem size at 9 years of age.

Traits of 50-year-old trees

The measures for trees from each provenance, except for Renge-dake (Sch. 21), were averaged at each plot to focus on the measures representative of a particular stand while ignoring variation among individual trees. We performed analysis of variance (ANOVA) for variables of the density (ha^{-1}), height (m), DBH (cm), and crookedness of stems, the width and length of branches, and the per-area stem cross-sectional area (m^2 ha^{-1}) at breast height and stem-volume index (m^3 ha^{-1}) using function anova in R 2.15.1. We used a linear model,

$$y_{ijk} = \mu + S_i + P_j + SP_{ij} + e_{ijk}, \tag{1}$$

where y_{ijk} is the variables at site i, of provenance j, and for replicate k; μ is the whole mean; S_i is the effect of site i; P_j is the effect of provenance j; SP_{ij} is the effect of interaction between site i and provenance j; and e_{ijk} is the error term of individual variables at site i, of provenance j, and for replicate k. The mean squares of the effects (MS_S, MS_P, and MS_{SP}) and error (MS_e) obtained from a random factor ANOVA are defined as

$$\begin{aligned} MS_S &= \sigma_e^2 + n\sigma_{SP}^2 + np\sigma_S^2 \\ MS_P &= \sigma_e^2 + n\sigma_{SP}^2 + ns\sigma_P^2 \\ MS_{SP} &= \sigma_e^2 + n\sigma_{SP}^2 \\ MS_e &= \sigma_e^2 \end{aligned} \tag{2}$$

with variance components of the effects (σ_S^2, σ_P^2, and σ_{SP}^2) and error (σ_e^2) and the number of levels for site $s = 3$ and provenance $p = 24$ and of replicates $n = ((4 - 8/24) + 4 + 3)/3$. We evaluated the variance components to compare the magnitude of the effects on the variables. We examined the statistical significance ($P < 0.05$) for the effects on the basis of F values with the degrees of freedom $F_S[s-1, (s-1)(p-1)] = MS_S/MS_{SP}$, $F_P[p-1, (s-1)(p-1)] = MS_P/MS_{SP}$, and $F_{SP}[(s-1)(p-1), sp(n-1)] = MS_{SP}/MS_e$).

We performed a principal component analysis for provenances with the number, height, DBH, and crookedness of stems and the width and length of branches at each site using function princomp in R 2.15.1. The six variables at individual plots were averaged for each provenance and then standardized. We characterized the stem and branch traits of the provenances in the nine regions according to the first and second principal components and loading of the six variables on the components.

Growth curves

We applied a hierarchical Bayesian model to a growth curve of the per-area stem-volume index (m^3 ha^{-1}) at each site. The index was available at three ages (12, 31 or 32, and 50 years) after the thinning. We assumed that the per-area stem-volume

index x_i at measurement i followed a normal (Gaussian) distribution with mean m_i and variance θ_{ti} at age t_i. The mean m_i is defined as

$$
\begin{aligned}
m_i &= a_i/[1 + \gamma \exp(-b_i z_i)] \\
a_i &= \alpha + \delta_{p_i} \\
b_i &= \beta + \varepsilon_{p_i},
\end{aligned}
\tag{3}
$$

where z_i is the age (years) of trees at measurement i. Parameters in these equations and their prior and hyper-prior distributions are defined in Table 3. We applied a logistic function to the growth curve, which is determined by three parameters, the maximum size, the growth rate, and the initial size. In addition to the parameters, we included random effects of provenances on the maximum size and the growth rate into the model. To estimate the parameters at each site, we carried out sampling from marginal posterior distributions in the Markov chain Monte Carlo (MCMC) method using JAGS 3.2.0 through function rjags 3–2 in R 2.15.1. We obtained posterior samples from three independent MCMC chains; 1,000 values were sampled at 50-step intervals after 5,000 burn-in MCMC steps. We confirmed convergence of MCMC calculations with the evaluation of Gelman and Rubin's R (Gelman et al. 2004) using function gelman.diag for all the parameters. At each site, we selected provenances with significantly high or low parameters of the random effects on the maximum size and the growth rate, of which 95 % range of the posterior distributions exceeded zero.

Correlations between climatic conditions and tree traits or stem growth

We examined whether climatic conditions were related with tree traits and stem growth among the provenances at each site. First, we estimated Spearman's correlation coefficient r

Table 3 Parameters and their prior or hyper-prior distributions in a hierarchical Bayesian model for growth curves of *Larix kaempferi* stem volume

Parameter	Name	Distribution	Mean	Variance
α	Maximum size	Gamma	1	10^2
β	Growth rate	Gamma	1	10^2
γ	Initial size	Gamma	1	10^2
δ_p	Random effects of provenance p on maximum size	Gaussian	0	$1/\rho$
ε_p	Random effects of provenance p on growth rate	Gaussian	0	$1/\tau$
θ_t	Variance parameter of size at age t	Gamma	1	10^2
ρ	Variance parameter of δ_p	Gamma	1	10^2
τ	Variance parameter of ε_p	Gamma	1	10^2

between the first or second principal component of the climatic variables and the first or second principal component of the stem and branch traits of 50-year-old trees. Second, we estimated r between that of the climatic variables and parameter δ or ε of the provenance effects on the maximum size or the growth rate (Table 3). We tested the correlation coefficients at each site using function cor.test and adjusted P values with Holm's method using function p.adjust in R 2.15.1.

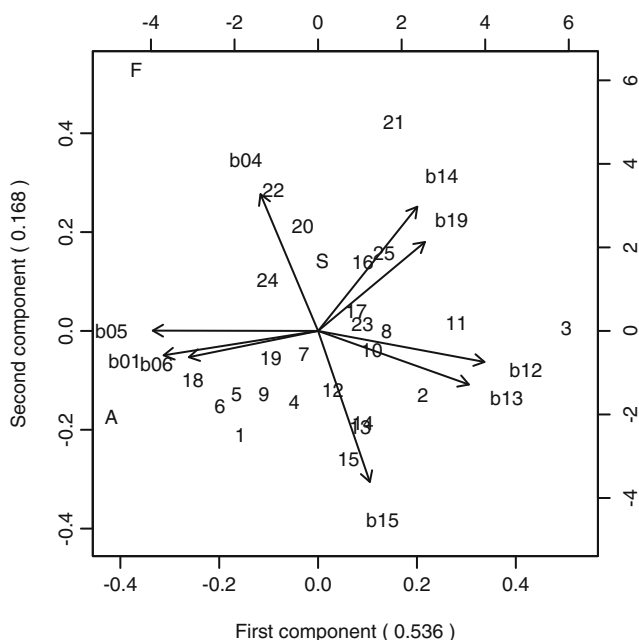## Results

Climatic conditions

Among the available 19 bio-climatic variables, nine variables (b01: annual mean temperature, b04: temperature seasonality, b05: maximum temperature of the warmest month, b06: minimum temperature of the coldest month, b12: annual precipitation, b13: precipitation of the wettest month, b14: precipitation of the driest month, b15: precipitation seasonality, and b19: precipitation of the coldest quarter) were selected to efficiently express the annual level and seasonal variation in temperature and precipitation and snowfall in winter. The first and second principal components of the variables contributed to 54 % and 17 %, respectively, of total variance in climatic conditions among the sites and provenances (Fig. 2). The first component is a contrast in temperature and precipitation and increases as temperature decreases and as precipitation increases. The second component reflects seasonal variation in temperature and precipitation and increases as temperature variation increases and as precipitation variation decreases, particularly as precipitation in the driest and coldest season increases.

Provenances (Sch. 20–22, 16, and 23–25) in northwestern regions (Kita Alps, Kusatsu, and Kiso; Fig. 1) had positive second components, indicating large temperature variation and small precipitation variation due to both much rainfall in summer and heavy snowfall in winter (Fig. 2). On the other hand, provenances (Sch. 1–3, 4, and 13–15) in southeastern regions (Fujisan, Kobushi-dake, and Nikko; Fig. 1) had negative second components, indicating the opposite pattern of climatic conditions due to much rainfall in summer but little snowfall in winter. The first components varied within the regions (Fig. 2), probably due to altitudinal variation (Table 1).

The test sites tended to be warmer and drier than the provenances (Fig. 2) because of lower altitudes at the sites (Table 2). Among the three sites, Asama and Fujisato were warmer than Shintaka at the highest altitude, and Asama had less variable temperature and more variable precipitation than Fujisato due to the geographic trends in climatic conditions.

Fig. 2 First and second principal components (contributions to total variance) of nine bio-climatic variables of provenances and test sites for *Larix kaempferi*. Numbers are Sch. numbers of provenances in Table 1. Letters *A*, *F*, and *S* are test sites Asama, Fujisato, and Shintaka, respectively, in Table 2. *Arrows* indicate loading of bio-climatic variables on components. *b01* annual mean temperature, *b04* temperature seasonality, *b05* maximum temperature of the warmest month, *b06* minimum temperature of the coldest month, *b12* annual precipitation, *b13* precipitation of the wettest month, *b14* precipitation of the driest month, *b15* precipitation seasonality, *b19* precipitation of the coldest quarter

Traits of 50-year-old trees

In the mean height and diameter and the density of 50-year-old stems at each plot, the effects of site and provenance on the variables were significant ($P<0.014$), but the effects of their interaction were not always significant ($0.023<P<0.597$; Table 4). The variance components were much larger in the site effects (70–81 %) than in the other effects (0–6 %;

Table 4). The stem height and diameter were largest in Asama, smallest in Shintaka, and intermediate in Fujisato, but the stem density showed the inverse trend (Table 2). All the effects on the per-area stem cross-sectional area and volume index at each plot were significant ($P<0.031$; Table 4). Because variations in the stem size and density among the sites were canceled out, the variance components for the stem cross-sectional area and volume were smaller in the effects of site (3–9 %) and interaction (8–12 %) than in the provenance effects (27–33 %; Table 4). The stem cross-sectional area was larger in Shintaka, but the stem volume was larger in Asama and Fujisato (Table 2). In the branch width and length and the stem crookedness averaged at each plot, the effects of site and provenance on the variables were significant ($P<0.001$) except for the provenance effects in the branch length ($P=0.069$), but the interaction effects were not significant ($0.050<P<0.834$; Table 4). The variance components for each variable were larger in the effects of site (22–31 %) and provenance (4–26 %) than in the interaction effects (0–6 %; Table 4). The branch width and length and the stem crookedness were largest in Asama (Table 2).

The first and second principal components of the stem and branch traits contributed to 38–42 % and 16–21 %, respectively, of total variance in the variables among the provenances (Fig. 3). At every site, the first component increased as the branch width and length and the stem diameter increased, and the second component increased as the stem height and diameter increased (Fig. 3). Loadings of the stem density and crookedness on the principal components varied among the sites. Thus, positive values in the first and second components indicate large size of trees. The provenances in region Fujisan (Sch. 1–3) in Asama and Fujisato (Fig. 3a, b) and in region Nikko (Sch. 13–15) in Shintaka (Fig. 3c) showed large tree size. As expected from the small effects of interaction between site and provenance, there was no evidence that provenances near each of the three sites exhibited large tree size at the respective sites (Sch. 17–19 in Fig. 3a,

Table 4 Number of levels, degree of freedom, and variance component percentage of effects and error for measures of stem and branch traits and stem mass per planted area in 50-year-old *Larix kaempferi* trees

	Site	Provenance	Site × Provenance	Error
No. of levels	3	24		
Degree of freedom	2	23	46	184
Variable	σ_S^2 (%)	σ_P^2 (%)	σ_{SP}^2 (%)	σ_e^2 (%)
Stem height	70.7***	3.0**	0.0 ns	26.3
Stem diameter at breast height	80.9***	5.3***	0.2 ns	13.6
Stem density	73.9***	3.3*	3.0*	19.8
Per-area stem cross-sectional area at breast height	3.0*	32.7***	11.6**	52.7
Per-area stem volume index	8.6***	27.4***	8.8*	55.2
Branch width	22.3***	25.6***	5.7 ns	46.4
Branch length	29.3***	4.9 ns	4.5 ns	61.3
Stem crookedness	31.0***	11.3***	0.0 ns	57.7

***$P<0.001$, **$0.001 \leq P<0.01$, *$0.01 \leq P<0.05$, ns $0.05 \leq P$
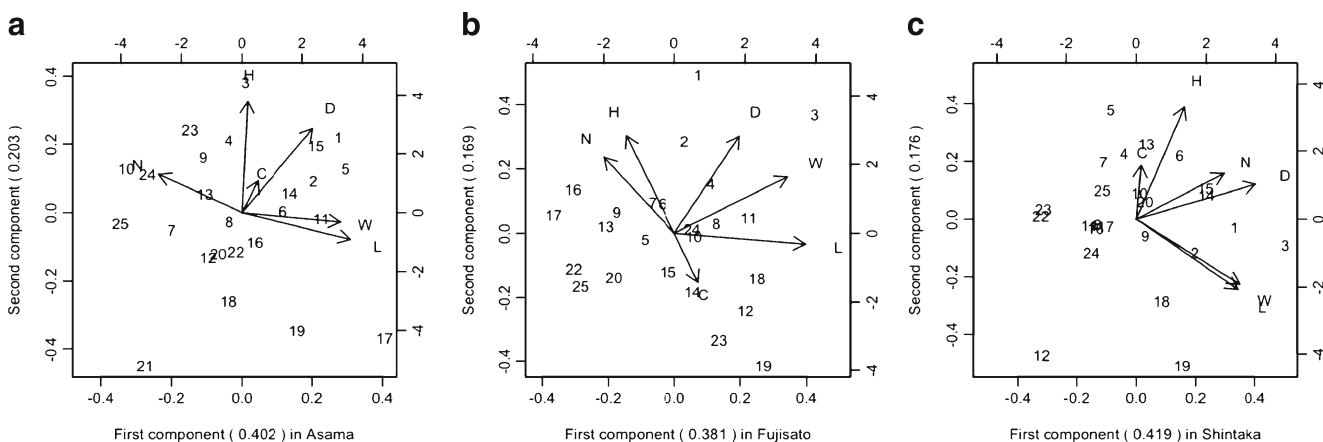
Fig. 3 First and second principal components (contributions to total variance) of six measures for stem and branch traits in provenances for *Larix kaempferi* at 50 years of age. *Numbers* are Sch. numbers of provenances in Table 1. Test sites are Asama (**a**), Fujisato (**b**), and Shintaka (**c**) in Table 2. *Arrows* indicate loading of measures on components. *H* height, *D* diameter at breast height, *N* density, *C* crookedness of stems, *W* width of branches, *L* length of branches

Sch. 16 and 20–22 in Fig. 3b, and Sch. 23–25 in Fig. 3c). The per-area stem cross-sectional area at breast height and stem-volume index were largest in regions Fujisan (Sch. 1–3), Kobushi-dake (Sch. 4), and Nikko (Sch. 13–15) and smallest in regions Minami Alps (Sch. 11–12) and Asama-yama (Sch. 17–19; Table 1). In Asama, provenance Renge-dake (Sch. 21) in region Kita Alps indicated the smallest cross-sectional area and volume index of stems per area (Table 1).

Growth curves

From the per-area stem-volume index at each plot at three ages (12, 31 or 32, and 50 years), growth curves were estimated for each provenance at each site (Fig. 4). Three MCMC chains sufficiently converged at every site ($1.02 < R < 1.04$), and unbiased samples of posterior distributions of the parameters were obtained from the chains. Based on the mean curve at each site, the maximum size was smaller and the growth rate was higher in Shintaka ($\alpha = 787$ m^3 ha^{-1} and $\beta = 0.214$ log(m^3 ha^{-1}) year^{-1}; Fig. 4c) than in Asama ($\alpha = 926$ m^3 ha^{-1} and $\beta = 0.192$ log(m^3 ha^{-1}) year^{-1}; Fig. 4a) and Fujisato ($\alpha = 963$ m^3 ha^{-1} and $\beta = 0.180$ log(m^3 ha^{-1}) year^{-1}; Fig. 4a, b).

In the growth curves of the per-area stem-volume index across the three sites, the provenances in regions Fujisan, Yatsugatake, and Nikko (Sch. 1, 2, 3, 6, 14, and 15) showed significantly larger maximum sizes, and the provenances in regions Mimani Alps, Asama-yama, Kita Alps, and Kiso
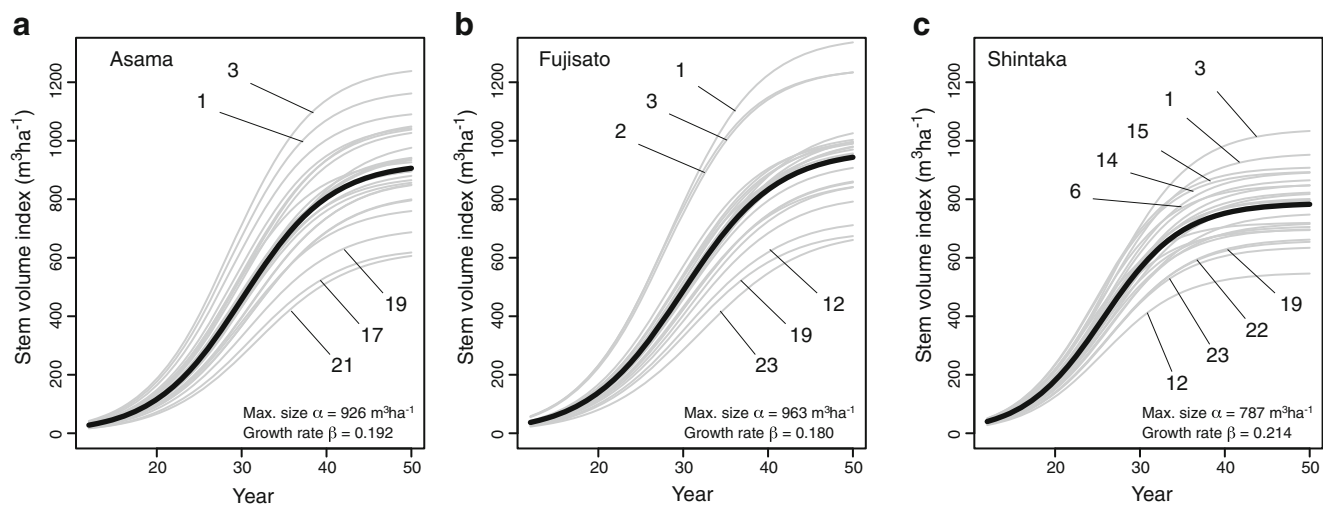
Fig. 4 Growth curves of stem-volume index for provenances at test sites for *Larix kaempferi*. *Black* and *gray curves* indicate mean and individual curves, respectively, for provenances at each site. *Numbers* indicating curves are Sch. numbers of provenances in Table 1, of which maximum size α significantly deviated from the mean at test sites Asama (**a**), Fujisato (**b**), and Shintaka (**c**)

(Sch. 12, 17, 19, 21, 22, and 23) exhibited significantly smaller maximum sizes (Fig. 4, Appendix 2). The growth rates did not significantly differ among the provenances at every site (Appendix 2).

### Correlations between climatic conditions and tree traits or stem growth

The first principal component of climatic variables in the provenances was not significantly correlated with tree traits ($P=1.000$ after Holm's adjustment for six multiple tests: the first and second principal components of trait variables at the three sites) and stem growth ($P=1.000$, the maximum size and growth rate of stems at the three sites). On the other hand, the second principal component of climatic variables was correlated, significantly at one or two sites, with the provenance effects on the maximum size ($0.009<P<0.245$) and growth rate ($0.001<P<0.245$) of the per-area stem-volume index and with the first principal component of the stem and branch traits of 50-year-old trees ($0.005<P<0.878$), but was not significantly correlated with the second principal component of the tree traits ($0.078<P<0.878$). At all the sites, the second principal component of climatic variables was negatively correlated with the first principal component of the tree traits ($-0.646<r<-0.220$) and with the provenance effects on the stem growth ($-0.707<r<-0.295$; Fig. 5). Thus, provenances with climatic seasonality of higher temperature variation and lower precipitation variation exhibited smaller stem diameter and smaller branches of 50-year-old trees as well as smaller maximun size and slower growth rate of stems.

Discussion

Climate conditions

The natural habitats of *L. kaempferi* are limited to the mountain range and fragmented into discontinuous alpine regions in central Japan (Toda and Mikami 1976) (Fig. 1). Thus, trait variation among provenances is expected because of random genetic drift in the fragmented habitats as well as divergent natural selection in heterogeneous environments across the mountain range. Alpine conifer species in central Japan also show genetic and phenotypic variations (Tsumura 2006). As compared with widely distributed Japanese conifers, such as *Cryptomeria japonica*, *Chamaecyparis obtusa*, and *Pinus parvifolia*, *L. kaempferi* showed a similar level of genetic differentiation between populations despite its narrow distributional range (Tsumura 2006). Alpine plant species, including *L. kaempferi*, have experienced climatic changes during the Pleistocene (Fujii and Senni 2006). Their distributional ranges are thought to have shifted to lower altitudes and expanded to continuously wide plains during glacial periods, but shifted to higher altitudes and retracted to fragmented alpine zones during inter-glacial periods (Takahara et al. 2000). The present climatic conditions may represent past climatic features during inter-glacial periods, when the *L. kaempferi* distributional range was restricted, and when genetic and phenotypic variations could evolve owing to genetic drift and natural selection. Therefore, the present climatic conditions seem to be related to factors driving trait variation.

The observed geographic patterns of climatic variables demonstrated a contrast across the *L. kaempferi* distributional
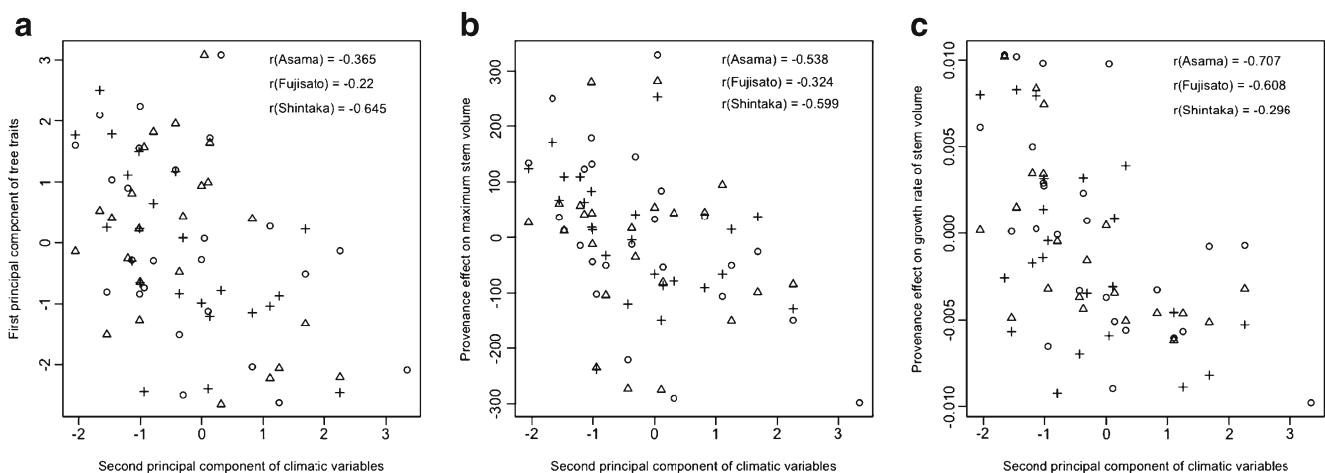
Fig. 5 Relationship beween second principal component of climatic variables in provenances (Fig. 2) and first principal component of stem and branch traits of 50-year-old trees (Fig. 3) (**a**) or effects of provenance on maximum size δ (**b**) and growth rate ε (**b**) of stem-volume index (Table 3, Appendix 2) in *Larix kaempferi* in Asama (*circles*), Fujisato (*triangles*), and Shintaka (*crosses*). Spearman's correlation coefficient was shown at each site

range between northwest and southeast (Fig. 2). Northwestern provenances show large temperature variation and small precipitation variation. Southeastern provenances exhibit the opposite pattern. These climatic patterns represent contrasting climates between northwest and southeast coastal sides of the Japanese mainland. On the other hand, the difference in altitude is likely to affect variation in the annual levels of temperature and precipitation within the geographic regions (Fig. 2). Climate is colder and wetter in provenances at higher altitudes. These geographic and altitudinal variations also explain climatic differences among the test sites. Climate in Shintaka at higher altitude is colder, whereas that in northwestern Fujisato is more variable in temperature, as compared with that in Asama.

Traits of 50-year-old trees

Stem height, diameter, and density of 50-year-old trees varied among the sites (Table 4). Because there were only three sites, these variations could occur due to random differences in environmental conditions among the sites. The variations, however, have a consistent trend. Stem size is larger at sites where stem density is lower (Table 2), suggesting a trade-off between survival and growth. Among the three sites, the stem size was highest in Asama and lowest in Shintaka (Table 2), the former site is warmer and drier than the latter. Thus, relatively high temperature and low precipitation in planted sites are likely to facilitate stem growth. In *L. decidua* in Italy, monthly maximum temperatures in June and July positively affected tree-ring growth, but monthly percipitation in June affected the growth negatively (Carrer and Urbinati 2004, 2006). Therefore, warmer and drier conditions during the growing season seem to enhance stem growth in larches. Such facilitated growth may result in intensive competition among trees and high mortality. On the other hand, the stem density was lowest in Asama and highest in Shintaka (Table 2). Asama has more marginal climatic conditions than does Shintaka with regard to typical climatic conditions found in most provenances (Fig. 2). These marginal conditions may lead to pest and disease damage since *L. kaempferi* is susceptible to various pests and diseases (Hayashi et al. 1998). Such damage may cause mortality directly and facilitate growth indirectly. Although the direction of causal relationship is unknown, our findings suggest that climatic conditions at planted sites affect survival and growth patterns of *L. kaempferi* trees.

As a consequence of the inverse trend between size and density of stems among the sites, variation in cross-sectional area and volume of stems per planted area was reduced among the sites (Table 4). Owing to the small site effect, the provenance effect on the per-area stem

mass had a large variance component (Table 4). The size of stems and branches and the per-area stem mass tended to be largest in provenances in regions Fujisan, Kobushi-dake, and Nikko (Table 1, Fig. 3), which are located in the eastern margin of the natural distributional range of *L. kaempferi* (Fig. 1). The results suggest that variation in tree size and per-area stem mass shows a geographic pattern associated with climatic conditions.

Variation in the traits at 50 years of age among the provenances was similar to those at two previous ages, 9 and 31 or 32 years, in the same provenance tests (Toda and Mikami 1976; Nagasaka et al. 2011). Thus, the provenance variations are correlated among the ages. In Europe and North America, however, different patterns in provenance variations were observed. In Canada, stem volume in a 19-year-old stand was measured for 20 Japanese provenances and largest in regions Kusatsu, Kiso, and Kobushi-dake (Park and Fowler 1983). In France, stem and branch traits of 12 provenances were assessed, but clear geographic patterns were not found (Paques 1996). These findings in foreign test sites differ from our results. This fact suggests that trait variations among provenances differ between test sites in foreign and native habitats. Therefore, interactions between planted sites and provenances can be important on a large geographic scale in spite of minor effects of the interactions observed in our test sites within the natural distributional range of *L. kaempferi* (Table 4).

Growth patterns and climate conditions

A logistic growth curve requires both convergence to a constant maximum size and a gradual decline in the growth rate as it approaches the maximum size (Tsoularis and Wallace 2002). These assumptions seem plausible but have not been evident in stem growth in larches. At our test sites, thinning was conducted at 12 years of age, which can affect growth curves. Growth curves of the per-area stem-volume index were estimated after the thinning, and the index at 12 years of age was obtained from the density of stems remaining after the thinning and the mean stem size at 9 years of age. Because the difference in the stem size between the ages of 9 and 12 years is relatively small, the estimated curves are unlikely to be biased. However, growth curves were estimated from the measures at only three ages and thus should be confirmed by additional data such as tree-ring analysis.

The estimated curves of stem growth differed among the three sites (Fig. 4). In Shintaka, the coldest site at the highest altitude, the estimated maximum size was the smallest, and the estimated growth rate is the highest. Alpine zones at high altitudes are stressful habitats with low temperatures and strong winds. Reduced tree size at such altitudes near the

forest limit or tree line is a well-known phenomenon (Paulsen et al. 2000), which is likely to result in the smallest maximum size observed at the highest altitude. Although it is difficult to explain the highest growth rate found at the highest altitude, this result suggests the potential of fast growth under cold conditions (Park and Fowler 1983; Paques 1996).

Eastern provenances, such as Fujisan and Nikko, show the highest estimates of the maximum size (Fig. 4), which corresponds to the variation observed among the provenances in the traits of 50-year-old trees. In Canada, growth curves of stem height from 9 to 29 years of age were estimated for 20 Japanese provenances using log-linear functions, and fast growth was found in regions Kiso and Kusatsu (Magnussen and Park 1991). Thus, stem growth variations among the provenances also differ between test sites in foreign and native habitats. In Finland, height growth of *L. gmelinii* and *L. sibirica* trees from provenances across the Eurasian continent was investigated at northern and southern test sites and showed latitudinal home-site advantage (northern provenances outgrew southern ones in the northern test site and vice versa) and disadvantage in provenances at high altitudes (Lukkarinen et al. 2010). Although these findings differ from our results, these studies suggest geographic and climatic factors of provenances affect stem growth traits.

The geographic pattern of variation in tree traits and stem growth among the provenances is associated with the contrasting climates between the opposite coastal sides of the Japanese mainland (Fig. 5) but is not related to the altitudinal variation in climatic conditions. Provenances in regions characterized by the climate on the southeast coastal side, such as Fujisan and Nikko, show high performance of stem and branch growth. In contrast, the northwesternmost provenance, Renge-dake, exhibits the contrary trend. The contrasting climatic conditions between the opposite coastal sides suggest that the growth traits have evolved under different climate conditions in the present post-glacial and past inter-glacial periods. In particular, climate on the northwest coastal side of the Japanese mainland is unique and characterized by wet winters due to heavy snowfall. This unique climate is known to have affected the genetic structure (Ohsawa and Ide 2011), life-history traits (Uemura 1989), and physiological and morphological characters (Tateishi et al. 2010) of forest trees. Compact crowns and stout stems with dense year-rings resulted from small stem diameter of the northwestern provenances may be suitable to survive with heavy snowfall becasue the weight and pressure of snow can damage tall stems and long branches. Thus, the northwestern climate might exert selection pressure on the growth strategy of *L. kaempferi*. However, it is not clear that growth traits could have diverged among the fragmented and heterogeneous habitats or that migration and different modes of selection might have interfered with trait divergence through climate changes during the Pleistocene.

Implications for tree breeding

Eastern provenances in the natural distributional range of *L. kaempferi* provide candidate breeding materials and additional plus trees with high performance in long-term stem growth. Because plus trees from the eastern provenances are still relatively rare (Kurinobu 2005), more superior trees can be selected from these provenances. In Japan, *L. kaempferi* was introduced from central Japan to Hokkaido, the northernmost island of Japan, at the beginning of the 1900s, and nearly 80 % of the timber of this species has been produced in Hokkaido (Koike et al. 2000). Most plus trees in Hokkaido were selected from the introduced populations (Koike et al. 2000). Thus, genetic diversity of the plus trees is currently narrow, and the additional plus trees can increase genetic variation to improve desirable traits. In Hokkaido, a hybrid larch between *L. gmelinii* var. *japonica* and *L. kaempferi* has become prevalent because of its heterotic advantages, such as fast juvenile growth, stem straightness, and relatively high resistance to gnawing by the vole *Myodes rufocanus bedfordiae* (Moriguchi et al. 2008). It is important to select additional plus trees for breeding materials to make such hybrid larches in Hokkaido, a major plantation region outside the natural distributional range of *L. kaempferi*. The minor effects of interaction between sites and provenances suggest that stable performance can be realized in different plantation sites. At test sites outside of central Japan, however, inconsistent trends in the performance of provenances were found, and thus, plantation in non-indigenous sites requires performance tests in these sites.

Appendix 1. Spatial arrangement of plots at test sites, Asama (a), Fujisato (b), and Shintaka (c)

Trees of each provenance (numbers indicate Sch. numbers in Table 1) were planted at each plot. Number of planted trees, planting matrix, and size of plots are shown. Shaded plots (a) were damaged due to a forest fire. Open plots (b, c) were not used for provenance tests.

a) Asama

25	22	23	21	24	22	7	2	17	12
2	1	3	4	5	1	6	11	16	21
13	11	14	15	12	15	20	5	25	10
18	17	20	19	16	3	13	18	8	23
7	8	9	6	10	9	4	24	19	14
9	24	4	14	19	4	1	5	3	2
13	3	18	8	23	15	12	13	11	14
12	22	7	2	17	23	21	24	22	25
1	11	6	21	16	9	7	6	10	8
25	20	5	15	10	20	16	19	17	18

North

12 columns
12 rows
21.6m × 21.6m

144 planted trees

b) Fujisato

North

19	23
14	8
4	18
24	3
9	13
17	16
2	
7	6
22	11
12	1
10	
15	
5	
20	
25	

7 columns
12 rows
21.6m × 12.6m

84 planted trees

4	1	5	3	2
15	12	13	11	14
23		24	22	25
9	7	6	10	8
20	16	19	17	18

			22
7	2	17	12
1	6	11	16
15	20	5	25	10
3	13	18	8	23
9	4	24	19	14
25	22	23		24
2	1	3	4	5
13	11	14	15	12
18	17	20	19	16
7	8	9	6	10

c) Shintaka

North

7 columns
12 rows
21.6m × 12.6m

84 planted trees

10	7	6	8	9		14	13	11	15	12
	15	5	10	20	25	16	6		11	1
7		1	19	25	13	14		8	2	20

5	4	2	3	1	25	24	23		22	18	16	17	20	19
2	17	7	22	12	23	3	13	18	8	24	4	14	19	9
11	10	23	17	4	5	24	18	12	6	15	16	9	3	22

Appendix 2. Estimated maximum size (α, δ) and growth rate (β, ε) parameters of per-area stem-volume index in *Larix kaempferi* in average (α, β) and in each provenance (δ, ε) at each test site

Table 5

Sch. no	Region	Asama α (m³ ha⁻¹)	Fujisato	Shintaka	Asama β (log(m³ ha⁻¹) year⁻¹)	Fujisato	Shintaka
		926.3 δ_P (m³ ha⁻¹)	969.3	787.2	0.192 ε_P (log(m³ ha⁻¹) year⁻¹)	0.180	0.214
1	Fujisan	251.3*	388.9*	170.8*	0.010	0.010	−0.003
2	Fujisan	178.7	279.5*	82.9	0.010	0.016	−0.001
3	Fujisan	329.3*	282.2*	253.8*	0.010	0.013	−0.006
4	Kobushi-dake	123.3	41.2	63.0	0.000	0.008	0.008
5	Yatsugatake	−44.1	−12.5	13.6	0.003	0.007	0.003
6	Yatsugatake	−14.7	56.9	108.6*	0.005	0.003	−0.002
7	Yatsugatake	−12.7	16.5	−4.6	0.002	−0.004	0.003
8	Yatsugatake	32.9	53.8	−66.4	−0.004	0.000	0.018
9	Yatsugatake	132.4	43.3	18.0	0.003	0.003	0.001
10	Yatsugatake	144.6	−35.2	41.0	0.001	−0.002	−0.003
11	Minami Alps	−53.7	−80.8	−86.7	−0.005	−0.003	0.001
12	Minami Alps	−102.3	−234.9*	−237.8*	−0.007	−0.003	0.000
13	Nikko	36.3	60.8	67.1	0.000	−0.005	−0.006
14	Nikko	12.7	11.6	109.3*	0.010	0.001	0.008
15	Nikko	133.6	26.9	124.0*	0.006	0.000	0.008
16	Kusatsu	−106.0	94.5	−66.7	−0.006	−0.006	−0.005
17	Asama-yama	−290.1*	43.5	−78.7	−0.006	−0.005	0.004
18	Asama-yama	−50.7	−103.7	−32.9	0.000	0.000	−0.009
19	Asama-yama	−220.9*	−273.1*	−119.9*	−0.003	−0.004	−0.007
20	Kita Alps	−25.8	−98.7	37.5	−0.001	−0.005	−0.008
21	Kita Alps	−298.2*	NA	NA	−0.010	NA	NA
22	Kita Alps	−149.4	−84.4	−128.1*	−0.001	−0.003	−0.005
23	Kiso	83.7	−275.2*	−148.9*	−0.009	−0.012	−0.003
24	Kiso	37.5	44.7	−90.4	−0.003	−0.005	0.013
25	Kiso	−50.7	−149.7	14.4	−0.006	−0.005	−0.009

The parameters are explained in Table 3

*95 % credible intervals exceed from zero

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