Morphological variation of the head characters in Solidago virgaurea L. inhabiting three mountains in central Honshu

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Toru Nishizawa^{1,4}, Eiichiro Kinoshita², Kimitaka Yakura¹ and Tatemi Shimizu³ : Morphological variation of the head characters in Solidago virgaurea L. inhabiting three mountains in central Honshu

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Abstract

The aims of this paper are (i) to obtain an overall variation pattern for the head morphology in Solidago virgaurea plants growing on Mt. Hakusan, Mt. Norikuradake and Mt. Yatsugatake, and (ii) to examine whether any boundaries can be found between plants growing at lower altitudes and those at higher altitudes as has been stated. Morphometric studies were performed. Sampling was undertaken at every 100 meters in altitude along mountain trails. Sample plants were collected from 16 sites on Mt. Hakusan, 11 sites on Mt. Norikuradake, and 12 sites on Mt. Yatsugatake. Ten plants were chosen randomly at each site. Thirteen morphological characters were measured and uni as well as multivaliate analyses were conducted. For most characters change was continuously observed site-by-site and there were significant differences among the sites. Two distinct clusters could be found by Principal Component Analysis, but the two clusters could not be recognized by a single character alone. They agree with Kitamura's taxonomic descriptions of subsp. *asiatica* and subsp. *leiocarpa* (1937, 1957).

Key words: Mt. Hakusan, Mt. Norikuradake, Mt. Yatsugatake, Principal Component Analysis, Solidago virgaurea.

Solidago virgaurea L. is a perennial herb widely distributing in the temperate and subarctic zones from Europe to East Asia and is exceedingly polymorphic. This species grows widely throughout Japan in different habitats such as open riverbeds, forest floors, sunny rocky places, grasslands, marshes, etc. at various sites from seashores to the alpine zone. Kitamura (1937, 1957) considered the shape and size of the involucre and involucral bracts the most important characters taxonomically and consequently recognized several intraspecific taxa. These have often been called a S. virgaurea complex because of the difficulty in taxonomic treatment, and much attention has been paid to the morphological variations and adaptations (Kawano and Takasu 1972; Kawano 1974; Takasu 1975; Hayashi 1976, 1977, 1978; Takasu et al. 1980; Abe and Takasu 1983; Suzuki and Teranuma 1986). These studies demonstrated that (i) some characters, such as leaf shape and size, show remarkably plastic variations under different light conditions, and (ii) on the contrary, the involucre and the involucral bracts exhibit little morphological variability under various ecological conditions.

As for S. virgaurea plants inhabiting the central and northern parts of Japan, Kitamura (1937, 1957) recognized two intraspecific taxa, subsp. asiatica Kitam. and subsp. leiocarpa (Benth.) Hultén, on the basis of herbarium specimens. Some morphometric and ecological studies support intraspecific differentiation. Hayashi (1976, 1978) conducted studies based on both herbarium specimens and mass-collected samples from several natural populations and found two morphologically distinguishable types. The two types differed in several characters of the involucral bracts. Of those characters, Hayashi's studies gave most emphasis to the validity of the inner/outer involucral bracts ratio for discriminating the two types. He reported that on Mt. Tateyama and the neighboring mountains one type grew at lower altitudes and the other type at higher altitudes. In addition, he stated that intermediate forms between the two types were found at about 1,500-1,700 m above sea level, where the montane zone bordered on the subalpine zone. Consequently, Hayashi concluded that two intraspecific taxa could be recognized, one type corresponding to subsp. asiatica and the other to subsp. leiocarpa. Nishizawa et al. (1997) collected sample plants every 100 m in altitude on Mt. Hakusan, from 1,200 to 2,500 m. They reported morphological changes in several head characters at about 1,700 or 1,800 m in altitude where the subalpine zone replaces the montane zone. Natori (1964) studied S. virgaurea growing on Mt. Yatsugatake from an ecological point of view. He showed that the dry weight of the aerial parts and that of the underground parts showed a diphase in an allometric relationship; plants growing at lower sites fall into one allometric growth pattern and those at higher sites fall into another one.

No evidence for intraspecific differentiation, however, has been found in studies based on cytological or molecular methods. Abe and Takasu (1983) collected plants from 13 populations, an elevational range from 2 m to 2,310 m in Toyama Prefecture, and reported that all of the samples examined had the same chromosome number, 2n=18, and the same karyotype. Nakamura et al. (1997) studied the cytological and genetic polymorphism of plants collected at eight sites, from 1,260 m to 2,670 m, on Mt. Hakusan. The chromosome number and the karyotype were the same for all of the plants examined. They also found no chromosomal or genetic polymorphism based neither on a fluorescence in situ, hybridization method nor on other methods, RAPD, concluding that no differentiation among the sites on Mt. Hakusan could be supported.

As mentioned above, the methods and morphological characters examined in the former studies were diverse. Lack of the common characters examined makes it hardly possible to compare the results among the study sites and to obtain an overall morphological variation pattern of S. *virgaurea* species. Thus, the aim of this paper is (i) to describe the full extent of morphological variability of head characters in *S. virgaurea* plants growing on Mt. Hakusan, Mt. Norikuradake and Mt. Yatsugatake, and (ii) to examine whether any boundaries can be found between plants growing at lower altitudes and those at higher altitudes as has been stated (Natori 1964; Hayashi 1976, 1978).

Materials and methods

Solidago virgaurea grows widely and continuously from the foot to the summit on Mt. Hakusan, Mt. Norikuradake and Mt. Yatsugatake. The locations of the three mountains are shown in Fig. 1. Mt. Hakusan and Mt. Norikuradake belong to the same climatic region characterized by heavy snowfall in winter, whereas Mt. Yatsugatake belongs to another climatic region characterized by low snowfall in winter (Miyawaki 1985).

Sample collections were carried out in the flowering seasons, from late August to mid-October, 1997. Sampling was undertaken every 100 meters in altitude along mountain trails. Sample plants were collected at 16 sites on Mt. Hakusan from Bettodeai (1,200 m) to the top of Ohnanjimine (2,684 m), 11 sites on Mt. Norikuradake from Norikurakogen (1,700 m) to the top of Kengamine (3,026 m), and 12 sites on Mt. Yatsugatake from Minoto (1,350 m) to the top of Amidadake (2,805 m).

Ten plants were randomly chosen at each site



Fig. 1. Locations of Mt. Hakusan, Mt. Norikuradake and Mt. Yatsugatake.

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where there was no evidence of artificial activities such as trampling or mowing. All heads on the main stem were collected and immediately put into a plastic bag filled with a 50% mixture of ethylalcohol and distilled water. The plant height and stem diameter at the ground level were measured before sampling. Voucher specimens were also collected from each site and have been deposited at the Herbarium, Kanazawa University (KANA).

Thirteen morphological characters were measured in this study (Table 1, Fig. 2). Since vegetative characters, such as the shape and dimensions of leaves, exhibit great plasticity in various environmental conditions (Kawano and Takasu 1972; Kawano 1974; Hayashi 1977), they were excluded. Preliminary statistical examinations showed no significant within-plant difference (one-way ANOVA) for any morphological characters of the head. Thus, the first three heads in the inflorescence were taken and measured, and a mean was calculated for each character. Sample materials were magnified twelve times with a Profile Projector Nikon V-20 A, and they were measured and recorded with a Data Processor Nikon DP-300.

Data analyses were performed by using the Statistical Analysis System, version 5 (SAS 1985). Analysis of Variance (ANOVA) for balanced data was carried out to compare the means among the sites on the same mountain using the GLM Procedure. Differences among

Table	1.	Morpho	logical	characters	employed
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DHA	Density of hairs on peduncle
DIN	Diameter of involucre
NIB	No. of involucral bracts per head
LII	Length of inner involucral bracts
LOI	Length of outer involucral bracts
WII	Width of inner involucral bracts
WOI	Width of outer involucral bracts
ΑΙΙ	Area of inner involucral bracts
AOI	Area of outer involucral bracts
NTF	No. of tubular flowers per head
NLF	No. of ligulate flowers per head
PLH	Plant height
DIS	Diameter of stem at base





Fig. 2. Diagrammatic illustrations of (a) capitulum, (b) inner involucral bract and (c) outer involucral bract of *Solidago virgaurea*. For abbreviations, see Table 1.

means were compared by the Tukey method at a significant level of 0.05. Principal Components Analysis (PCA) of the correlation matrix for 13 variables was also performed by using the PRIN-COMP Procedure. Analyses were executed on the mainframe computer of the Information Processing Center, Kanazawa University.

Results

1. Univariate data description

Means and standard deviations of the thirteen morphological characters are summarized in the Appendix. For most characters, change was continuously observed site-by-site, and there were significant differences among the sites. Multiple comparison by the Tukey method reveals that plants growing at lower sites differ significantly from those growing at higher sites with respect to many characters (Fig. 3). No significant differences were found in two characters, NIB on Mt. Norikuradake and Mt. Yatsugatake and WII on Mt. Yatsugatake.

Localities	Altitude	DHA	DIN	NIB	LII	LOI	WII	WOI	AII	AOI	NTF	NLF	PLH	DIS
Mt. Hakusan	2684 m 2600 m 2500 m 2400 m 2200 m 2000 m 1900 m 1800 m 1700 m 1500 m 1400 m 1300 m													
	р	**	**	**	**	**	**	**	**	**	**	**	**	**
Mt. Norikuradake	2700 m 2600 m 2500 m 2400 m 2300 m 2100 m 2100 m 1900 m 1800 m 1700 m	 	 + +	NS		 		! 	*) 1 1 1 1 1 1 1	 	 	**	 	
Mt. Yatsugatake	2700 m 2600 m 2500 m 2400 m 2300 m 2200 m 2000 m 1900 m 1900 m 1700 m 1350 m				**	**	NS							

Fig. 3. Multiple comparison by Tukey method. Vertical bars represent the range of means that are not significantly different. *, p < 0.001; **, p < 0.0001; NS, not significant.

Table 2. Coefficients of the variable in the principal components in *Solidago virgaurea*. The first, second and third principal components account for 66.4, 12.7 and 8.3% of the total variation, respectively. Boldface numbers show higher values in the first principal component. For abbreviations, see Table 1

Variable	Principal components							
variable	First	Second	Third					
DHA	0.234	-0.142	-0.152					
DIN	0.328	0.029	-0.105					
NIB	0.239	0.346	-0.345					
LII	0.307	-0.033	0.037					
LOI	0.332	-0.073	0.050					
WII	0.292	-0.100	0.341					
WOI	0.319	-0.145	0.171					
ΑΙΙ	0.299	-0.170	0.293					
AOI	0.309	-0.203	0.213					
NTF	0.323	0.143	-0.162					
NLF	0.230	0.476	-0.288					
PLH	-0.188	0.324	0.563					
DIS	0.110	0.632	0.373					

2. Multivariate analysis

PCA was applied to the data set. The eigenvector of the first three principal components, each element of which represents a coefficient of the variable in the principal components, are shown in Table 2. Of those variables, LOI, DIN, NTF and WOI have a high absolute value in the first component, indicating that these variables have more intensive effects on the component score. The first principal component accounts for 66.4% of the total variation, the second for 12.7%, and the third for 8.3%. Therefore, about 80% of the total variation is due to the first two principal components. A plot of principal component scores of morphological variables is shown in Fig. 4. This ordination shows that the first principal component axis can separate two clusters, while the second axis cannot.

One cluster spreads in the positive quadrants of the first axis and the other cluster occupies the negative quadrants. On Mt. Hakusan plants growing at sites from 1,200 m to 1,800 m in altitude form one cluster and those from 1,900 m to 2,700 m form the other cluster. Similarly, plants from 1,700 m to 1,900 m form one cluster and those from 2,000 m to 2,700 m form the other cluster on Mt. Norikuradake, and on Mt. Yatsugatake one cluster is from 1,300 m to 2,200 m and the other is from 2,300 m to 2,700 m.

Discussion

This study reveals an entire spectrum of variations in head morphology of *S. virgaurea* plants growing on Mt. Hakusan, Mt. Norikuradake and Mt. Yatsugatake. PCA demonstrates that two clusters are recognizable in the three mountains (Fig. 4). Each cluster has a close relationship to the altitude of the sampling sites. Plants growing below one altitude form one cluster and those above that altitude form the other cluster. This is the case for the three mountains, although the altitudes of border lines differ for each mountain.

Concerning S. virgaurea growing on Mt. Yatsugatake, it has already been demonstrated that the dry weight of the aerial parts and underground parts show a diphase in an allometric relationship, in which plants growing above 2,500 m in altitude fall into one allometric relationship and those growing below 2,400 m into the other one(Natori 1964). This result suggests that two different types exist on Mt. Yatsugatake in terms of the growth pattern and design of a plant body. In our results, one cluster is made up of plants growing below 2,200 m and the other cluster consists of plants growing above 2,300 m. The fact that the two independent studies, each of which is based on an ecological and a morphological viewpoint, reach almost the same conclusion clearly indicates that two different types exist in *S. virgaurea* plants growing on Mt. Yatsugatake.

The three clusters in the negative quadrants of the first axis, which were recognized independently on each mountain, overlap with one another, indicating that they form one comprehensive cluster, and the three in the positive quadrants likewise form another cluster (Fig. 4). It is assumed that each cluster, which inhabits different altitudes on the mountains, the lower sites and higher sites, corresponds to an actual biological unit, a taxon. Although Natori (1964) did not refer to classification, his results clearly showed the existence of the two taxa characterized by differences in gross morphology and/or life history strategies in terms of the differences in resource allocation patterns. Thus one conclusion is that two taxa are recognizable in S. virgaurea growing on the three mountains.

This study clearly shows that a single charac-



Fig. 4. Scatter diagram drawn on the first and second principal components. The first and second principal components account for 66% and 13% of the total variation, respectively. Squares indicate Mt. Hakusan, circles Mt. Norikuradake, and triangles Mt. Yatsugatake. The numeral next to each symbol indicates altitude ($\times 100$ m).

ter alone is not useful for discriminating the two clusters (=taxa) recognized by PCA. PCA shows that LOI, DIN, NTF and WOI have a higher absolute value of coefficient in the first component (Table 2), indicating that these variables have larger influences on the component score. Of these characters, LOI, which has been used as a key character in the classification of this species (Kitamura 1937, 1957), also has the highest value in this study. Thus, in our results LOI is

also considered the most important one as a diagnostic character. LOI alone can discriminate the given two clusters on Mt. Norikuradake, while it cannot on Mt. Hakusan and Mt. Yatsugatake (Fig. 5 a). This is true of DIN, NTF and WOI (Figs. 5 b, c, d).

These results indicate that even if the two taxa exist in *S. virgaurea* growing on Mt. Hakusan and Mt. Yatsugatake, we cannot tell them apart based on a single character. Hayashi



Fig. 5. Changes in means (solid circle) with standard deviations (solid line) against altitude : (a) length of outer involucral bract, (b) diameter of involucre, (c) no. of tubular flower, (d) width of outer involucral bract, and (e) ratio of inner/outer involucral bract. H, Mt. Hakusan; N, Mt. Norikuradake; Y, Mt. Yatsugatake. Broken line shows the boundary of clusters distinguished in PCA (see Fig. 4).

(1976, 1978) pointed out the validity of the inner /outer involucral bracts ratio for discrimination. In this study, this ratio could not fully delimit the two taxa (Fig. 5 e). On Mt. Norikuradake, this ratio can delimit the two taxa. On Mt. Hakusan, two types were recognized by this ratio, but they do not fully agree with the clusters recognized in PCA. This ratio does not work at all in discriminating the two taxa on Mt. Yatsugatake. It is noteworthy that NTF, which has gained little attention, can serve as a diagnostic character.

According to our results, the two taxa are characterized as follows: Plants of one taxon have heads with 5–10 tubular flowers, involucre 2–3 mm across, outer involucral bracts 1–2 mm long, 0.5-1 mm wide, grow at lower places; and plants of the other taxon have heads with 15–25 tubular flowers, involucre 3–4 mm across, outer involucral bracts 2–4 mm long, 0.8-1.5 mm wide, grow at higher places (Figs. 5 a, b, c, d; Appendix).

It is most likely that the two taxa (clusters) recognized in PCA are equivalent to intraspecific ones, because (i) they cannot be distinguished by a single character alone but be recognized by a multivariate method and (ii) no differentiation can be found between the two in terms of cytology and genetics (Abe and Takasu 1983; Nakamura et al. 1997). The two taxa generally agree with Kitamura's diagnosis of *S. virgaurea* subsp. *asiatica* and subsp. *leiocarpa* (1937, 1957).

Kawano (1974) argued that S. virgaurea occurring in the Japanese Islands originally grew on floors of deciduous forest and since then had gained various habitats, such as lowland grasslands, maritime pine forests, subalpine coniferous forests, alpine meadows, etc. Considering present geographical ranges of subsp. asiatica and subsp. leiocarpa in the Eurasian Continent and adjacent regions, however, our study indicates that the two taxa, which may have originated at different areas in the Continent, have come into contact on mountains in central and northern parts of Honshu, Japan. The geographical distribution and elevational habitat segregation of the two taxa are the outcome of geohistorical events. As for subsp. leiocarpa, the present distribution in higher elevations in the

central and northern parts of Honshu may be the final result of several repetitions of an advance to the Japanese Islands from northern regions in the cooler periods and a subsequent retreat in the warmer periods, while present distribution in various habitats for subsp. *asiatica*, everywhere from seashores to low mountains, may be the outcome of the latest advance in the warmer periods.

Subsp. *leiocarpa* is likely to exhibit larger morphological variability than subsp. *asiatica* within a mountain, and also shows great variations among mountains (Figs. 3, 4, 5). One of the reasons for this may be due to the fact that subsp. *leiocarpa* is restricted to narrow areas which are isolated from one another in higher altitude of mountains in central Honshu, while subsp. *asiatica* inhabits various habitats, everywhere from seashore to mountains. Thus, subsp. *leiocarpa* may have adapted to the environmental conditions characteristic of each mountain.

As Hayashi (1976) pointed out, intermediate plants were found at sites where the two taxa had got in contact. They are found on Mt. Hakusan and Mt. Yatsugatake (Figs. 3, 5; Appendix). The intermediate plants, which obscure the boundary and cause difficulty in classification, may be hybrids between the two taxa. However, this is a mere assumption and requires a survey of variation patterns for subsp. *asiatica* and subsp. *leiocarpa* growing in the Continent.

In conclusion, we can recognize the two taxa in *S. virgaurea* growing on Mt. Hakusan, Mt. Norikuradake and Mt. Yatsugatake. However, this result is based on a restricted number of sample plants from only three mountains in central Honshu, Japan. When we consider the differentiation of this species, even if the focus is restricted to the local differentiation around the Japanese Islands and adjacent regions, we have to take account of the worldwide variation patterns. Thus further studies should include plants sampled from wider areas and more mountains on the Japan Islands and adjacent regions.

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西沢 徹^{1,4}・木下栄一郎²・矢倉公隆¹・清水建美³: 本州中部地方の3山岳に生育するアキノキリンソ ウの頭花形態の変異

本研究の目的は、(1) 白山, 乗鞍岳, 八ヶ岳に 生育するアキノキリンソウ(広義)の頭花形態の変 異を生育地の下部から上部にわたって明らかにする こと、(2) 従来言われてきたように低地から山地 帯に生育する集団と亜高山帯から高山帯に生育する 集団間に差異が認められるかどうかを明らかにする。 ことである。試料の採取は各山岳とも登山道に沿っ て標高100mごとに行ない,1地点あたり10個体 を無作為に採取した。採取場所は白山16ヶ所,乗 鞍岳11ヶ所,八ヶ岳12ヶ所である。13形質につ いて計測し分散分析と主成分分析を行った。その結 果,ほとんどの形質では標高に沿った連続的な変異 が見られ,それらに関して低地と高地の生育地の間 で有意な差が認められた。この結果は3山岳に共 通であった。主成分分析ではいずれの山岳でも標高 に対応した2つの明確なクラスターが認められた。 2つのクラスターは単独の形質では判別できないこ となどいくつかの理由によりそれぞれ別の種内分類 群を表していると考えるのが最も合理的である、と 結論した。

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Appendix. Means and standard deviations of the thirteen morphological characters of *Solidago virgaurea*. For abbreviations, see Table 1.

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Localities	Altitude	Ν	DHA(/0.25 mm ²)	DIN (mm)	NIB	LII (mm)	LOI (mm)
	2684 m	10	10.63 ± 1.70	4.16 ± 0.32	$22.35 {\pm} 2.40$	5.42 ± 0.28	4.17 ± 0.34
	2600 m	10	10.67 ± 1.27	$4.36{\pm}0.38$	$22.07 {\pm} 1.88$	$5.42 {\pm} 0.25$	3.67 ± 0.50
	2500 m	10	9.93 ± 1.69	3.77 ± 0.44	$20.37 {\pm} 2.13$	5.13 ± 0.45	$3.19{\pm}0.38$
	2400 m	10	8.87 ± 1.38	3.53 ± 0.22	18.97 ± 1.49	$5.03{\pm}0.44$	$3.66{\pm}0.51$
	2300 m	10	$10.53 {\pm} 2.28$	$3.68 {\pm} 0.30$	$20.73 {\pm} 2.81$	$5.26 {\pm} 0.29$	$3.09{\pm}0.41$
	2200 m	10	9.77 ± 2.37	$3.80\!\pm\!0.31$	$19.27 {\pm} 2.23$	5.53 ± 0.49	$3.68 {\pm} 0.55$
	2100 m	10	$8.47 {\pm} 2.09$	$3.18{\pm}0.16$	17.83 ± 1.70	5.15 ± 0.55	$3.21{\pm}0.38$
Mt. Hakusan	2000 m	10	8.10 ± 1.94	$3.25 {\pm} 0.37$	20.23 ± 2.34	$5.41{\pm}0.34$	$3.28 {\pm} 0.62$
	1900 m	10	10.13 ± 1.88	$3.09{\pm}0.34$	18.83 ± 1.91	$4.80{\pm}0.38$	$2.89{\pm}0.47$
	1800 m	10	11.53 ± 2.77	$2.71 {\pm} 0.49$	17.35 ± 2.17	$4.35{\pm}0.32$	$2.52{\pm}0.34$
	1700 m	10	$6.17 {\pm} 2.50$	2.55 ± 0.29	16.37 ± 1.55	$4.50{\pm}0.48$	$1.91{\pm}0.48$
	1600 m	10	5.73 ± 3.10	2.65 ± 0.26	$15.87 {\pm} 2.01$	$4.17 {\pm} 0.43$	$1.62{\pm}0.40$
	1500 m	10	3.73 ± 1.19	$2.45 {\pm} 0.26$	15.43 ± 1.71	$4.35{\pm}0.44$	$1.55 {\pm} 0.13$
	1400 m	10	3.97 ± 1.86	$2.55 {\pm} 0.17$	17.03 ± 1.72	$4.38{\pm}0.59$	$1.54 {\pm} 0.31$
	1300 m	10	$3.90 {\pm} 2.13$	$2.26 {\pm} 0.27$	$15.47 {\pm} 2.54$	$4.24{\pm}0.46$	$1.58 {\pm} 0.28$
	1200 m	10	$3.57 {\pm} 2.35$	$2.33 {\pm} 0.27$	16.47 ± 1.75	$4.39{\pm}0.46$	$1.59 {\pm} 0.29$
F-value	•		F _{15,144} =18.91**	F _{15,144} =45.98**	F15,144=12.35**	F _{15,144} =13.56**	F15,144=49.73**
	2700 m	10	13.43 ± 1.93	4.12 ± 0.44	18.92 ± 3.18	5.49 ± 0.57	4.67 ± 0.55
	2600 m	10	11.97 ± 1.79	$4.16{\pm}0.45$	17.10 ± 3.81	5.92 ± 0.53	$5.22 {\pm} 0.74$
	$2500~{ m m}$	10	12.83 ± 1.32	4.05 ± 0.39	19.30 ± 2.17	$5.46 {\pm} 0.39$	$4.19{\pm}0.60$
	2400 m	10	11.93 ± 1.91	4.05 ± 0.55	19.60 ± 1.65	$5.56 {\pm} 0.60$	4.37 ± 0.64
	2300 m	10	9.70 ± 1.99	$4.09 {\pm} 0.39$	19.83 ± 3.12	$5.56 {\pm} 0.58$	$3.63 {\pm} 0.88$
Mt. Norikuradake	2200 m	10	$8.47 {\pm} 2.59$	$3.47 {\pm} 0.55$	$20.53 {\pm} 4.00$	5.20 ± 0.50	$3.17 {\pm} 0.51$
	2100 m	10	$8.37 {\pm} 2.00$	$3.46{\pm}0.24$	18.80 ± 1.66	$5.11 {\pm} 0.35$	$2.96{\pm}0.32$
	2000 m	10	8.63 ± 1.39	$3.61 {\pm} 0.33$	18.93 ± 1.50	$5.79 {\pm} 0.64$	$3.39 {\pm} 0.56$
	1900 m	10	7.23 ± 1.59	$2.45 {\pm} 0.20$	$17.63 {\pm} 1.72$	$4.72 {\pm} 0.59$	$1.77 {\pm} 0.26$
	1800 m	10	$7.47 {\pm} 2.52$	2.40 ± 0.32	16.90 ± 1.74	4.68 ± 0.55	$1.95 {\pm} 0.45$
	1700 m	10	$9.53 {\pm} 3.05$	$2.36{\pm}0.13$	16.93 ± 1.37	$4.59 {\pm} 0.53$	$1.64 {\pm} 0.24$
F-value	•		F10,99=11.37**	F10,99=36.65**	F10,99=2.47	F _{10,99} =7.27**	F10,99=47.59**
	2700 m	10	10.07 ± 1.83	369 ± 0.34	18 83+1 36	537 ± 037	334 ± 030
	2600 m	10	10.66 ± 1.03	3.33 ± 0.37	17.80 ± 2.85	5.01 ± 0.01	3.15 ± 0.53
	2500 m	10	9.27 ± 1.28	3.35 ± 0.31 3.37 ± 0.46	18.00 ± 2.00	5.37 ± 0.37	3.46 ± 0.55
	2000 m 2400 m	10	8.07 ± 2.30	3.52 ± 0.43	18.67 ± 1.41	5.07 ± 0.01 5.12 ± 0.31	3.11 ± 0.88
	2300 m	10	8.03 ± 2.67	3.52 ± 0.48	18.37 ± 3.33	5.12 ± 0.01 5.28 ± 0.49	3.09 ± 0.54
Mt. Yatsugatake	22000 m	10	11.10 ± 2.45	3.08 ± 0.54	18.87 ± 2.67	5.25 ± 0.13 5.05 ± 0.52	2.48 ± 0.44
mi. Taisugatake	2100 m	10	840 ± 2.40	3.09 ± 0.54	18.40 ± 1.92	5.05 ± 0.02 5.15 \pm 0.49	2.40 ± 0.49 2.51 ± 0.49
	2100 m	10	10.47 ± 2.20	2.52 ± 0.23	10.40 ± 1.02 18.23+2.93	4.80 ± 0.40	1.88 ± 0.18
	1900 m	10	957 ± 2.14	2.02 ± 0.23 2.42+0.29	17.57 ± 1.85	4.73 ± 0.40	1.00 ± 0.10 1.85 ± 0.23
	1800 m	10	10.10 ± 2.02	2.56 ± 0.22	20.70 ± 1.00	4 78+0 47	1.00 ± 0.20 1.79 ± 0.97
	1700 m	10	777 ± 9.69	2.00 ± 0.20 2.40 ± 0.10	1757 ± 9.14	4.65+0.49	1.85+0.22
	1950 m	10	1.11 ± 2.02 19.69 ± 2.82	2.40±0.10	17.01 ± 2.14	4.00-0.42	1.00 ± 0.20 1.88 ± 0.91
	1990 III	10	12.03-3.00	2.00±0.29	11,10-4,10	4.40.4044	1.00-0.21
F-value			$F_{11,108}=3.64*$	$F_{11,108}=15.82^{**}$	F11,108=1.22	$F_{11,108}=5.27**$	F11,108=21.88**

*p <0.001 , **p <0.0001 .

WII (mm)	WOI (mm)	AII (mm²)	AOI (mm²)	NTF	NLF	PLH (cm)	DIS (mm)
0.86±0.09	1.02 ± 0.16	$3.74{\pm}0.32$	$3.46 {\pm} 0.44$	23.47 ± 3.53	8.67 ± 1.51	19.6± 2.37	3.08 ± 0.33
$0.89{\pm}0.12$	1.12 ± 0.10	$4.18 {\pm} 0.54$	$3.16 {\pm} 0.52$	$24.17 {\pm} 4.18$	10.47 ± 1.30	22.4 ± 5.25	3.05 ± 0.71
$0.88 {\pm} 0.17$	$1.04 {\pm} 0.19$	$3.73{\pm}0.60$	$2.59{\pm}0.50$	$19.58 {\pm} 4.10$	8.37 ± 1.13	$27.8\pm$ 5.49	$3.16{\pm}0.65$
$0.87{\pm}0.12$	1.20 ± 0.13	$3.57 {\pm} 0.72$	3.34 ± 0.67	19.27 ± 1.40	7.83 ± 1.10	25.4 ± 5.91	$2.94 {\pm} 0.59$
$0.83{\pm}0.11$	1.02 ± 0.13	$3.46 {\pm} 0.47$	$2.34{\pm}0.44$	20.33 ± 3.58	8.60 ± 1.22	24.7 ± 4.92	$2.84 {\pm} 0.36$
0.84 ± 0.11	$1.18{\pm}0.13$	3.83 ± 0.35	$3.21{\pm}0.65$	17.83 ± 3.95	8.33 ± 1.71	36.0 ± 3.86	$3.45 {\pm} 0.56$
$0.84 {\pm} 0.13$	$0.99{\pm}0.15$	$3.72 {\pm} 1.40$	$2.33{\pm}0.46$	14.90 ± 1.84	7.40 ± 1.49	$33.1\pm$ 7.28	3.02 ± 0.52
$0.86 {\pm} 0.06$	1.13 ± 0.13	$3.55 {\pm} 0.39$	$2.52{\pm}0.58$	17.33 ± 4.46	9.33 ± 1.44	43.7 ± 5.54	3.22 ± 0.37
$0.86 {\pm} 0.08$	1.01 ± 0.11	3.08 ± 0.28	$2.13{\pm}0.52$	16.37 ± 3.23	8.17 ± 1.69	41.3 ± 6.55	$3.18 {\pm} 0.47$
$0.74 {\pm} 0.06$	$0.88 {\pm} 0.07$	$2.31 {\pm} 0.36$	$1.43 {\pm} 0.33$	14.67 ± 3.12	6.83 ± 1.60	37.2 ± 11.28	$2.72{\pm}0.60$
$0.69 {\pm} 0.17$	$0.76 {\pm} 0.17$	$2.74 {\pm} 0.68$	$1.09{\pm}0.43$	9.43 ± 3.04	5.93 ± 0.98	35.2 ± 8.97	2.18 ± 0.46
$0.75{\pm}0.12$	$0.71{\pm}0.12$	$2.63{\pm}0.34$	$0.95{\pm}0.29$	7.27 ± 1.36	$5.63{\pm}0.91$	36.6 ± 8.95	$2.15{\pm}0.44$
$0.66 {\pm} 0.09$	$0.68 {\pm} 0.12$	$2.54 {\pm} 0.37$	$0.88 {\pm} 0.20$	6.63 ± 1.16	5.73 ± 1.04	$41.3\pm$ 8.79	$2.46{\pm}0.38$
$0.72{\pm}0.06$	$0.68{\pm}0.10$	$2.71{\pm}0.54$	$0.87 {\pm} 0.25$	7.57 ± 1.39	5.73 ± 0.62	45.0 ± 17.37	2.53 ± 0.90
$0.74 {\pm} 0.11$	$0.65 {\pm} 0.14$	$2.78 {\pm} 0.54$	$0.86 {\pm} 0.31$	6.97 ± 1.45	5.07 ± 0.97	$33.2\pm~7.18$	2.53 ± 0.59
$0.72{\pm}0.07$	$0.66 {\pm} 0.11$	$2.80{\pm}0.39$	$0.94 {\pm} 0.30$	7.00 ± 1.87	5.23 ± 1.07	37.7 ± 7.57	$2.40{\pm}0.53$
F15,144=5.02**	F15,144=23.67**	F15,144=9.62**	F15,144 =48.49 **	F15,144=44.00***	F15,144=16.47**	F15,144=9.23**	F13,126=5.54**
1.04 ± 0.08	1.51 ± 0.12	4.80 ± 0.74	$5.35 {\pm} 0.95$	21.03 ± 5.19	5.63 ± 1.79	16.5 ± 4.62	$1.99 {\pm} 0.52$
$1.09 {\pm} 0.15$	$1.65 {\pm} 0.21$	$5.12 {\pm} 0.86$	6.23 ± 1.26	$18.40 {\pm} 5.27$	5.97 ± 1.77	22.5 ± 4.99	2.49 ± 0.50
$1.00 {\pm} 0.13$	$1.38 {\pm} 0.15$	4.40 ± 0.68	4.29 ± 0.99	21.27 ± 3.88	7.07 ± 2.16	23.2 ± 4.78	$2.65 {\pm} 0.58$
1.04 ± 0.10	1.43 ± 0.16	$4.54 {\pm} 0.70$	4.66 ± 1.70	21.50 ± 3.82	7.57 ± 1.56	28.1 ± 4.20	$2.62 {\pm} 0.94$
$0.91 {\pm} 0.14$	1.19 ± 0.16	$4.10 {\pm} 0.92$	3.09 ± 1.04	18.17 ± 4.11	7.50 ± 1.00	37.6 ± 5.76	$2.31 {\pm} 0.49$
$0.81 {\pm} 0.11$	$1.15 {\pm} 0.13$	$3.45{\pm}0.40$	$2.69 {\pm} 0.55$	16.77 ± 4.52	7.73 ± 2.24	48.7±13.39	$3.12 {\pm} 0.60$
$0.88 {\pm} 0.08$	1.14 ± 0.08	$3.57 {\pm} 0.25$	$2.31 {\pm} 0.38$	15.30 ± 1.77	6.93 ± 1.12	34.0 ± 5.37	2.33 ± 0.54
$0.88 {\pm} 0.07$	$1.23 {\pm} 0.15$	$3.94 {\pm} 0.68$	$2.87 {\pm} 0.73$	$16.57 {\pm} 2.97$	$6.60 {\pm} 0.75$	46.8 ± 8.12	2.83 ± 0.45
0.82 ± 0.10	0.69 ± 0.12	$3.29{\pm}0.43$	$0.96 {\pm} 0.25$	8.53 ± 1.32	5.07 ± 0.41	54.2 ± 9.46	$2.53{\pm}0.31$
$0.73 {\pm} 0.11$	0.81 ± 0.16	$3.99 {\pm} 0.58$	$3.41 {\pm} 1.15$	8.20 ± 1.48	$4.97{\pm}0.78$	42.0 ± 6.96	$2.34 {\pm} 0.52$
$0.75 {\pm} 0.06$	$0.66 {\pm} 0.09$	$3.07{\pm}0.41$	$0.93{\pm}0.20$	8.53 ± 0.82	5.07 ± 0.58	75.4 ± 17.98	$3.18 {\pm} 0.47$
F10,99=13.52**	F10,99=51.74**	F10,99=10.32**	F10,99=31.80**	F10,99=21.26**	F10,99=5.64**	F10,99=37.21**	F10,99=4.09**
0.78±0.11	$1.02 {\pm} 0.13$	$3.40{\pm}0.35$	2.66 ± 0.28	18.83 ± 2.99	6.70 ± 1.04	23.60 ± 6.92	$2.02{\pm}0.21$
$0.80{\pm}0.16$	$0.99 {\pm} 0.23$	$3.69 {\pm} 0.85$	$2.42{\pm}0.80$	$15.43 {\pm} 3.34$	6.50 ± 1.28	$31.80\pm~7.19$	$2.39{\pm}0.52$
$0.75 {\pm} 0.11$	$1.10{\pm}0.16$	$3.36{\pm}0.55$	2.79 ± 0.75	$16.67 {\pm} 4.60$	6.43 ± 1.07	$30.20\pm\ 6.83$	$1.90{\pm}0.38$
0.73 ± 0.11	$0.97 {\pm} 0.15$	$3.20{\pm}0.51$	2.43 ± 0.96	16.23 ± 3.15	7.13 ± 3.00	$29.80 \pm \hspace{0.1cm} 2.35$	1.94 ± 0.29
$0.82{\pm}0.07$	$1.12{\pm}0.15$	$3.69{\pm}0.51$	$2.67{\pm}0.56$	14.30 ± 3.80	6.73 ± 1.00	$30.90\pm~5.82$	$2.14 {\pm} 0.37$
$0.68 {\pm} 0.07$	$0.82{\pm}0.12$	3.09 ± 0.44	$1.59 {\pm} 0.42$	12.57 ± 3.72	6.67 ± 1.09	$31.10\pm\ 8.12$	2.04 ± 0.40
$0.69 {\pm} 0.12$	$0.88 {\pm} 0.17$	$3.18{\pm}0.62$	$1.77{\pm}0.52$	11.73 ± 2.13	6.67 ± 0.97	27.40 ± 4.50	$1.63 {\pm} 0.26$
$0.72{\pm}0.10$	$0.75 {\pm} 0.09$	$2.89{\pm}0.37$	$1.15 {\pm} 0.19$	9.27 ± 1.80	$5.43 {\pm} 0.90$	$33.20\pm~5.07$	$1.93{\pm}0.28$
$0.73{\pm}0.05$	$0.80{\pm}0.10$	$2.78 {\pm} 0.45$	$1.23\!\pm\!0.24$	8.43 ± 1.32	5.07 ± 0.56	28.30 ± 5.46	$1.58{\pm}0.19$
$0.76 {\pm} 0.13$	$0.69{\pm}0.10$	$3.20{\pm}0.54$	$1.09 {\pm} 0.19$	$9.07 {\pm} 1.04$	5.37 ± 0.95	41.20 ± 10.85	$2.48{\pm}0.52$
$0.75 {\pm} 0.17$	$0.70 {\pm} 0.19$	$2.85{\pm}0.36$	$1.17{\pm}0.22$	8.03 ± 1.06	$4.90{\pm}0.65$	41.40 ± 9.26	$2.24{\pm}0.55$
$0.80{\pm}0.12$	0.85 ± 0.14	$3.20{\pm}0.54$	$1.09{\pm}0.19$	9.43 ± 1.46	$5.37{\pm}0.64$	$31.80\pm\ 6.39$	$1.79 {\pm} 0.31$
F11,108=1.45	F11,108=9.96**	F11,108=3.18*	F11,108=18.60**	F11,108=17.78**	F11,108=6.72**	F11,108=7.47**	F11,108=5.81**