北海道礼文華峠におけるブナ分布北限域孤立個体群 の立地と植生

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Introduction

Fagus crenata Blume is a representative canopy tree species of the cool temperate forests of Japan. Fagus crenata populations on the northern range front are scattered among the eastern mountains adjacent to the Kuromatsunai Lowland (approximately 42°40'N, 140° 20'E) on the northern Oshima Peninsula, Hokkaido (Tatewaki 1948, 1958). Some F. crenata populations, such as Tsubamenosawa and Sannosukesawa in the Horobetsu Mountains, near the Sea of Japan, are relatively well known, and several ecological/vegetation studies have been carried out in these populations (Kobayashi and Watanabe 2003; Namikawa et al. 2010; Tatewaki 1958; Watanabe 1987). On the other hand, F. crenata populations near Uchiura Bay (on the Pacific Ocean side) have not been well documented. Although F. crenata populations were once recorded in the region upstream of the Kamiraiba River in the town of Kuromatsunai (Tatewaki 1948) and in the Rebun region near the Opukesu River (currently named the Ofukishi River) in the town of Toyoura (Furuhata 1932), their exact locations have not been

confirmed (Kito 2001, 2003, 2008).

Under such circumstances, we found *F. crenata* trees on the rocky peaks in the Rebunge Pass near State Highway 37 in the spring of 2010, and a field investigation was carried out to record the current vegetation structure of the *F. crenata* population. An objective of this paper is, therefore, to clarify the vegetation, the size structure, and the soil conditions of the isolated *F. crenata* population at Rebunge Pass, Toyoura, Oshima Peninsula, Hokkaido. The habitat and vegetation characteristics of this isolated population are also discussed.

Study site description

The *F. crenata* population is located around Rebunge Pass, within the limits of Toyoura, Hokkaido (Fig. 1). The population is located on rocky ridges approximately 300 m north of the northeast end of the Rebun tunnel on State Highway 37 (42°36′19" N., 140°33′30" E.) (Figs. 2 and 3). The minimum horizontal distance between the study site and Uchiura Bay is approximately 2.5 km.

The following data are from the nearby me-

teorological station (AMeDAS) in Ookishi (8 m ASL), located 7.9 km east-southeast of the study site: mean annual temperature (1979 – 2000), 7.3°C; annual precipitation (1979 – 2000), 1,198 mm; annual hours of sunlight (1986 – 2000), 1,501; maximum snow depth (1983 – 2000), 85 cm (Japan Meteorological Agency 2010). The estimated Warmth Index (Kira 1948, 1977) at the study site (at 200 m ASL) was 52.5°C · month with a lapse rate of 0.6°C/100 m. The geology of the site is tertiary, Pliocene, and Frebeshi volcanics (hypersthenesaugite-andesitic agglomerate with andesitic tuff) (Doi et al. 2001).

Materials and methods Vegetation description

An actual vegetation map (Ito and Haruki 1981) was used to identify the vegetation on a 1:50,000 scale. Within the area of the *F. crenata* population (approximately 1.7 ha), a vascular plant list and the approximate height of vegetation layers were recorded. It would have been useful to set up quadrats in the field for

quantitative vegetation description; however, due to the steepness of the rocky ridges at the site, we were not able to establish them. Therefore, the vegetation description in this study is more or less qualitative. The nomenclature follows Yonekura and Kajita (2003). The field investigation was carried out on April 26 and July 22, 2010.

Fagus crenata distribution and measurement

We searched for F. crenata trees at the study site, using binoculars from several points with a magnification of 8 to $10 \times$. Fagus crenata trees were easy to identify when they began flushing prior to the other species in early spring. The location and elevation of each F. crenata tree were recorded by GPS (Garmin GPSmap 60CSx). The girth at breast height (GBH) for each F. crenata tree was measured to within 1 mm after the species had been identified. The diameter at breast height (DBH) was calculated as GBH/3.14.

Soil sampling

Soil was sampled at 5 points at the study

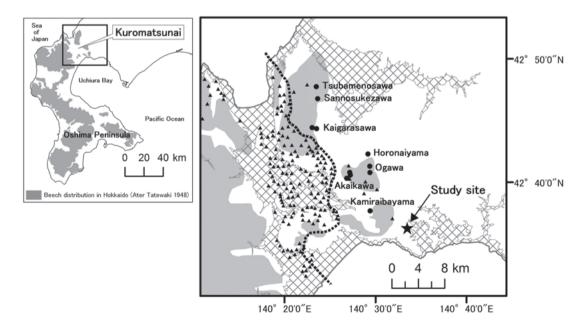


Fig. 1. Distributions of Fagus crenata in Hokkaido (after Tatewaki 1948) (left) and locations of major F. crenata populations on the northern range front (right). ★: The study site at Rebunge Pass; ●: major F. crenata populations on the range front; ▲: other F. crenata populations reported by Kito (2001, 2003, 2008). Gray shaded areas indicate F. crenata distribution after Tatewaki (1948), and gray lattice areas indicate elevations of less than 100 m. The dashed curve line shows the range frontline for continuous F. crenata distribution by Kito (2003, 2008).

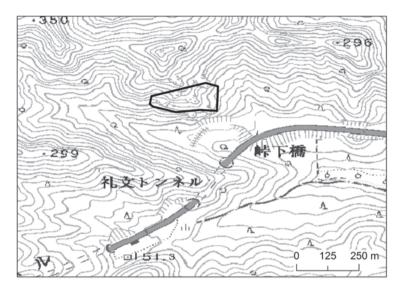


Fig. 2. Location of the Rebunge Pass *Fagus crenata* population (area surrounded by black bold lines). The area was approximately 1.7 ha, and the vascular plant list was recorded within the area. Map source is 1/25,000 "Rebungetouge" (Geographical Survey Institute 2001).



Fig. 3. Distant view of the study site. Trees indicated by two black arrows are Fagus crenata individuals.

site to perform soil chemical analyses. Each sampling point was set on the line transect at 10m intervals from higher to lower elevation. Soil was sampled from each of the three soil layers (0–5, 5–10, and 10–15 cm in depth). The soil pH, Total C, Total N, C/N ratio, NH₄-N, and NO₃-N were analyzed in the laboratory at the Faculty of Environmental Earth Science, Hokkaido University.

Results

Vegetation description

The national actual vegetation map (Ito and Haruki 1981) identified the study site as a lower conifer/broad-leaved mixed forest. The lower part of the slope adjacent to the rocky ridges is an artificial plantation of *Abies sachalinensis* (F. Schmidt) Mast.

We recorded 50 vascular plant species within 30 families (Table 1). On the rocky ridge, vegetation was hard to recognize except for the canopy and herb layers. The vegetation coverage on the rocky ridge was approximately 20%. Fagus crenata canopy trees on the rocky ridge were mixed with Quercus crispula Blume, Magnolia obovata Thunb., and Betula platyphylla Sukaczev var. japonica (Mig.) H. Hara. The tree height of the canopy ranged from approximately 8 to 10 m. The herb layer (less than 0.8 m) was represented by Carex blepharicarpa Franch., Artemisia keiskeana Mig., Lepisorus ussuriensis (Regel et Maack) Ching var. distans (Makino) Tagawa, Vaccinium japonicum Mig., V. oldhamii Mig., and Toxicodendron radicans (L.) Kuntze subsp. orientale (Greene) Gillis.

The relatively steep slope (30~35°) adjacent to the rocky ridges supported trees of F. crenata, Quercus crispula, Betula platyphylla var. japonica, and Acer pictum Thunb. (including A. pictum Thunb. subsp. mayrii (Schwer.) H. Ohashi) at the canopy layer (8–16 m in height). At the sub-canopy layer (2–8 m) were recorded Carpinus cordata Blume, Acer pictum, Abies sachalinensis, Alnus viridis (Chaix) Lam. et DC. subsp. maximowiczii (Callier) D. Löve, Viburnum furcatum Blume ex Maxim., Cerasus sargentii (Rehder) H. Ohba, and a few trees of F. crenata; however, no species was particu-

larly dominant. At the shrub layer (0.8–2 m), Sasa senanensis (Franch. et Sav.) Rehder was recorded as the dominant species. Other species at the shrub layer consisted of Cephalotaxus harringtonia (Knight ex Forbes), K. Koch var. nana (Nakai) Rehder, Viburnum furcatum, and Hydrangea paniculata Siebold. At the herb layer (less than 0.8 m), Skimmia japonica Thunb, var. intermedia Komatshu f. repens (Nakai) Ohui was the dominant species, followed by Daphniphyllum macropodum Miq. subsp. humile (Maxim. ex Franch. et Sav.) Hurus or Blechnum niponicum (Kunze) Makino (Table 1). The vegetation coverage on the slope was approximately 80%.

Fagus crenata distribution

We found 44 *F. crenata* trees with a height of 1.3 m or more scattered within an area of approximately 1.7 ha. Thirty-nine of the trees were situated on the rocky ridges and only five on the relatively steep slopes adjacent to the ridges (Fig. 4). The *F. crenata* trees were at elevations between 196 and 275 m ASL. DBH class distribution showed a moderate bimodal L-shape with a peak at 0–10 cm and 20–30 cm in DBH on the rocky ridge (Fig. 5A) and a disjunct bimodal shape on the slope (Fig. 5B). Old *F. crenata* cupules were found on the ground on the rocky ridge. In addition, three fallen *F. crenata* trees approximately 20–30 cm in DBH were observed on the rocky ridge.

Soil conditions

The soil at the study site was generally slightly moist to moist but, locally, slightly dry. Soil depth for the A and B layers was less than 18 cm, and the major root systems spread no more than 20 cm in depth.

The soil pH was slightly acidic, between 5.4 and 5.5 (Table 2). The total C gradually changed from 9.2% at the lower level to 14.7% at the surface level. The total N was lower at the lower level (0.6%) than at the surface level (1.0%). The C/N ratio was relatively high, between 14 and 15, and was consistent among the three levels. NH_4-N+NO_3-N showed relatively similar values within the same level.

Table 1. Flora list of the study site at Rebunge Pass

科名	Family	和名	Latin name
チャセンシダ科	Aspleniaceae	トラノオシダ	Asplenium incisum Thunb.
		コタニワタリ	Asplenium scolopendrium L.
シシガシラ科	Blechnaceae	シシガシラ	Blechnum niponicum (Kunze) Makino
ウラボシ科	Polypodiaceae	ミヤマノキシノブ	$Lepisorus\ ussuriensis$ (Regel et Maack) Ching var. $distans$ (Makino) Tagawa
イヌガヤ科	Cephalotaxaceae	ハイイヌガヤ	Cephalotaxus harringtonia (Knight ex Forbes) K. Koch var. nana (Nakai) Rehder
マツ科	Pinaceae	トドマツ	Abies sachalinensis (F. Schmidt) Mast.
カバノキ科	Betulaceae	ミヤマハンノキ	$Alnus\ viridis$ (Chaix) Lam. et DC. subsp. $maximowiczii$ (Callier) D. Löve
		ヒメヤシャブシ	Alnus pendula Matsum.
		ダケカンバ	Betula ermanii Cham.
		シラカンバ	Betula platyphylla Sukaczev var. japonica (Miq.) H. Hara
		サワシバ	Carpinus cordata Blume
ブナ科	Fagaceae	ブナ	Fagus crenata Blume
		ミズナラ	Quercus crispula Blume
モクレン科	Magnoliaceae	ホオノキ	Magnolia obovata Thunb.
キンポウゲ科	Ranunculaceae	カラマツソウ	Thalictrum aquilegiifolium L. var. intermedium Nakai
ユキノシタ科	Saxifragaceae	ノリウツギ	Hydrangea paniculata Siebold
		ツルアジサイ	Hydrangea petiolaris Siebold et Zucc.
		エゾアジサイ	Hydrangea serrata (Thunb.) Ser. var. yesoensis (Koidz.) H. Ohba
		イワガラミ	Schizophragma hydrangeoides Siebold et Zucc.
バラ科	Rosaceae	アズキナシ	Aria alnifolia (Siebold et Zucc.) Decne.
		オオヤマザクラ	Cerasus sargentii (Rehder) H. Ohba
		ナナカマド	Sorbus commixta Hedl.
ユズリハ科	Daphniphylla- ceae	エゾユズリハ	$Daphniphyllum\ macropodum\ {\it Miq.}$ subsp. $humile\ ({\it Maxim.}\ ex\ {\it Franch}\ et\ {\it Sav.})$ Hurus.
ミカン科	Rutaceae	ツルシキミ	Skimmia japonica Thunb. var. intermedia Komatsu f. repens (Nakai) Ohwa
ウルシ科	Anacardiaceae	ツタウルシ	Toxicodendron radicans (L.) Kuntze subsp. orientale (Greene) Gillis
カエデ科	Aceraceae	ハウチワカエデ	Acer japonicum Thunb.
		アカイタヤ	Acer pictum Thunb. subsp. mayrii (Schwer.) H. Ohashi
		イタヤカエデ	Acer pictum Thunb. subsp. pictum
モチノキ科	Aquifoliaceae	ツルツゲ	Ilex rugosa F. Schmidt
ニシキギ科	Celastraceae	コマユミ	Euonymus alatus (Thunb.) Siebold f. striatus (Thunb.) Makino
ブドウ科	Vitaceae	ヤマブドウ	Vitis coignetiae Pulliat ex Planch.
シナノキ科	Tiliaceae	シナノキ	Tilia japonica (Miq.) Simonk.
ジンチョウゲ科	Thymelaeaceae	ナニワズ	Daphne jezoensis Maxim.
スミレ科	Violaceae	スミレsp.	Viola sp.
ウコギ科	Araliaceae	コシアブラ	$Chengiopanax\ sciadophylloides\ (Franch.\ et\ Sav.)\ C.\ B.\ Shang\ et\ J.\ Y$ Huang
		ハリギリ	Kalopanax septemlobus (Thunb.) Koidz.
イチヤクソウ科	Pyrolaceae	ベニバナイチヤクソウ	Pyrola asarifolia Michx. subsp. incarnata (DC.) A. E. Murray
ツツジ科	Ericaceae	ミヤマホツツジ	Cladothamnus bracteatus (Maxim.) T. Yamaz.
		ハナヒリノキ	Eubotryoides grayana (Maxim.) H. Hara
		アクシバ	Vaccinium japonicum Miq.
		ナツハゼ	Vaccinium oldhamii Miq.
モクセイ科	Oleaceae	アオダモ	Fraxinus lanuginosa Koidz. f. serrata (Nakai) Murata
スイカズラ科	Caprifoliacea	オオカメノキ	Viburnum furcatum Blume ex Maxim.
キク科	Asteraceae	イヌヨモギ	Artemisia keiskeana Miq.
		ミヤマアキノキリンソウ	Solidago virgaurea L. subsp. leiocarpa (Benth.) Hultén
ユリ科	Liliaceae	ツクバネソウ	Paris tetraphylla A. Gray
イネ科	Poaceae	クマイザサ	Sasa senanensis (Franch. et Sav.) Rehder
		オオバザサ	Sasa megalophylla Makino et Uchida
カヤツリグサ科	Cyperaceae	ショウジョウスゲ	Carex blepharicarpa Franch.
		ヒカゲスゲ	Carex lanceolata Boott



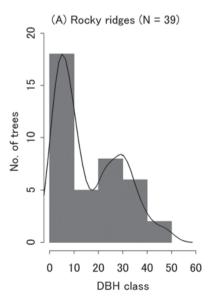
Fig. 4. Internal view of the Rebunge Pass study site. The largest tree in the photo is a Fagus crenata tree with diameter at breast height (DBH) of 40.9 cm.

Discussion

Phytogeographical position of the F. crenata population at Rebunge Pass

Fagus crenata populations along Uchiura Bay are conspicuously isolated (Tatewaki 1948; Kito 2001, 2003, 2008). Although Furuhata (1932) reported the existence of a F. crenata population in the regions upstream of the Opukesu River, no details regarding its location were confirmed. The present study clarified that the northern range front for F. crenata along the Pacific coast is at least at Rebunge Pass. The Rebunge Pass F. crenata population is located approximately 10 km east of the range frontline for the continuous F. crenata distribution depicted by Kito (2003) (Fig. 1). This information shows that the isolated F. crenata populations at this northern range front are in alignment with other isolated populations such as the Tsubamenosawa F. crenata population, the Sannosuke F. crenata population, the Horonaiyama F. crenata population, and the Ogawa F. crenata population (Fig. 1).

The study site abuts a plantation forest of *Abies sachalinensis* at the lower part of the study site. This fact gives rise to the possibility that *F. crenata* trees once grew on the site currently under tree plantation. Although there



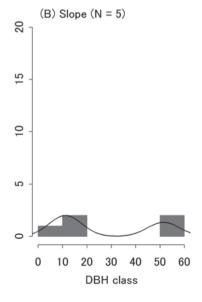


Fig. 5. Histogram of diameter at breast height (DBH) with a density curve for Fagus crenata at the Rebunge Pass study site: (A) trees on the rocky ridges and (B) trees on the slopes.

Table 2. Results of soil analysis at Rebunge Pass (mean \pm SD, n = 5)

Depth (cm)	0 - 5	5 - 10	10 - 15
pH (H ₂ O)	5.4 ± 0.3	5.5 ± 0.2	5.5 ± 0.1
Water content (%)	107.2 ± 94.8	69.8 ± 23.4	70.3 ± 24.8
NH_4 -N (mg/kg)	5.0 ± 6.0	3.5 ± 2.3	3.0 ± 0.9
NO_3 -N (mg/kg)	5.8 ± 3.1	2.6 ± 0.8	3.0 ± 1.4
NH_4+NO_3 (mg/kg)	10.9 ± 8.4	6.1 ± 2.8	6.0 ± 1.7
Loss of ignition (%)	30.6 ± 17.2	19.5 ± 5.3	19.2 ± 5.8
Total C (%)	14.7 ± 7.9	9.5 ± 3.6	9.2 ± 4.1
Total N (%)	1.0 ± 0.5	0.6 ± 0.3	0.6 ± 0.3
C/N ratio	15.1 ± 2.0	15.1 ± 2.2	14.4 ± 1.1

is no doubt that the *F. crenata* population at the Rebunge Pass is an isolated population, the past population might have been somewhat larger than the present one.

Floristic characteristics of the *F. crenata* populations at Rebunge Pass

The main floristic feature of this study site is that the plants recorded were mainly those growing on the Sea of Japan side or the inland part of Hokkaido between the southern Oshima Peninsula and Cape Soya. Some of these species are within the floristic group categorized by Uemura and Takeda (1987): (1) Arachniodes standishii group, Cephalotaxus harringtonia var. nana; (2) Leptorumohra quadripinnata group, Daphniphyllum macropodum subsp. humile, Skimmia japonica var. intermedia f. repens, Blechnum niponicum, and Asplenium scolopendrium L.

On the other hand, even though the study site is only 2.5 km inland from the Pacific Ocean (i.e., Uchiura Bay), no typical species growing on the Pacific coast from the southern part of Oshima Peninsula to the Kushiro region, such as Carpinus laxiflora (Siebold et Zucc.) Blume or Ostrya japonica Sarg., were recorded. Furthermore, no other typical temperate tree species, such as Quercus serrata Murray, Castanea crenata Siebold et Zucc., or Aesculus turbinata Blume, were recorded in this region (Kawahara et al. 2009). It is, therefore, noteworthy that the flora of the study site is characterized by species that tend to distribute on the Sea of Japan side of the peninsula. These findings led us to the conclusion that the species composition of the F. crenata population at Rebunge Pass is influenced by the Sea

of Japan-type climate, which is the same as that of the other *F. crenata* populations on the northern range front.

Habitat conditions of the *F. crenata* population at Rebunge Pass

This study clarified that most F. crenata trees establish on rocky ridges at Rebunge Pass. Moreover, the DBH class distributions of the F. crenata trees showed a slightly bimodal L shape on the rocky ridges (Fig. 4). This finding suggests that the site conditions on the rocky ridges with shallow soil deposits still allow F. crenata to grow at least up to 40 cm in DBH (Fig. 4). At around the northern range front, there are other F. crenata populations established on rocky ridges (such as the upstream area of Akaikawa and Kamiraibayama, in the town of Kuromatsunai). The fact that F. crenata establishes not only on slopes or ridges with thick soil layers but also on rocky ridges with shallow soil may be a unique feature of the area around the northern range because F. crenata usually establishes on slopes with deep and moderately moist conditions.

A similar habitat condition, in which *F. crenata* grew on steep rocky slopes of 60° by penetrating between rocks, was reported from the Tomari River basin, western Shimamaki region, *ca.* 20 km southwest from the Kuromatsunai Lowland (Tatewaki 1958). In the literature, it was speculated that substrate containing limestone, which differs from that in the present study, might have allowed *F. crenata* to grow.

Another exception was reported in Kanagawa, Kanto region: *F. crenata* trees grew on rocky slopes in Mt. Kintoki (Fujii et al. 2003). These slopes, on which saplings of young *F. crenata*

trees grow, have soil deposits less than 15 cm. Fujii et al. (2003) argue that the area is often shrouded by fog and this foggy environment retains moisture in the air that enables *F. crenata* to grow.

Similarly, in the vicinity of Rebunge Pass, fog frequently forms from Uchiura Bay in summer (Suttsu Weather Station 2008). Moreover, regional rainfall should also enable *F. crenata* to grow in the Rebunge Pass area. However, this foggy environment is not the only explanation for the establishment of the *F. crenata* population at Rebunge Pass because there are other *F. crenata* populations on the rocky ridges of the northern range front.

As is shown in the flora list, no conifer trees other than Abies sachalinensis were recorded, and no trees of A. sachalinensis were competing against F. crenata trees at the study site. This relative absence of conifer trees at the study site may allow F. crenata trees to establish on the rocky ridge. Rocky ridges in the temperate zone in Honshu southwards are often occupied by various conifer trees, such as Chamaecyparis obtusa (Siebold et Zucc.) Endl., Pinus parviflora Siebold et Zucc. var. pentaphylla (Mayr) A.Henry, Sciadopitys verticil-

lata (Thunb.) Siebold et Zucc., Tsuga sieboldii Carrière, Thuja standishii (Gordon) Carrière and Thujopsis dolabrata (L.f.) Siebold et Zucc. var. hondae Makino (e.g., Nozaki and Okutomi 1990; Murakami 2005). In the southern Oshima Peninsula in Hokkaido, Pinus parviflora var. pentaphylla, A. sachalinensis, and Thujopsis dolabrata var. hondae occur on the ridge part, and F. crenata grows on the adjacent lower part of slope (Hukusima et al. 1984). In the vicinity of the Kuromatsunai Lowland, Pinus parviflora var. pentaphylla and Thujopsis dolabrata var. hondae do not distribute, and only A. sachalinensis does. The actual distribution map showed that A. sachalinensis distributes throughout Hokkaido (e.g., Horikawa 1976) and A. sachalinensis often grew in F. crenata forests in Oshima Peninsula; however, their dominance was always low (Hukusima et al. 1984). The species distribution model for A. sachalinensis estimated that the Oshima Peninsula has less chance for the species to grow than other parts of Hokkaido (Tanaka et al. 2009). Moreover, previous forest statistics (Matsuda 1936) have shown that the cumulative volume of A. sachalinensis in the national forest was lower in Oshima Peninsula, including the Kuro-

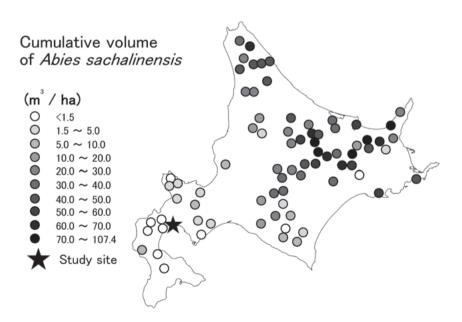


Fig. 6. Cumulative volume of *Abies sachalinensis* (m³ / ha) at each of the 76 national forest management districts in Hokkaido (modified and depicted from Matsuda (1936)).

matsunai area, than in the northern or eastern parts of Hokkaido (Fig. 6), which is in good agreement with the findings of Hukusima et al. (1984) and Tanaka et al. (2009). In the 1930s, almost all national forests in Hokkaido were considered natural forests; in other words, the proportion of artificial plantation forests was very small. Nevertheless, relatively smaller cumulative volumes of *A. sachalinensis* in southern Hokkaido have been observed through time, according to the forest statistics (e.g., Hokkaido 1964, 2004).

On the other hand, the present study showed that the soil chemical conditions, such as soil pH or inorganic nitrogen at Rebunge Pass (Table 2), did not differ much from other *F. crenata* forests nationwide (Haruki et al. 2009, 2010). Considering the discussion above, it is concluded that the establishment of *F. crenata* trees on the rocky ridges at Rebunge Pass became possible mainly because of (1) the suitable temperature and humidity during the growing season and (2) the relative absence of competitive conifer tree species on the rocky ridges.

Acknowledgments

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植牛

筆者らはブナの分布北限域における最前線孤立個体群を太平洋から水平距離で2.5km内陸に位置する豊浦町礼文華峠の岩峰上及びその周辺で発見した。これはブナの天然分布個体群の中でも太平洋側における最北限の個体群であると考えられた。付近のアメダスのデータによれば、年平均気温7.3℃、年降水量1,198 mm、最大積雪深85cmであった。現地の暖かさの指数WIは52.5℃・月と推定された。

ブナの分布、植生と立地の状況を明らかにするために現地調査を行った結果、以下の知見を得た.(1) 岩峰上に生育する胸高以上のブナは約1.7 haの範囲(標高196~275 m)に39本生育し、胸高直径階分布は緩やかなL字型を示し、10 cm以下の個体が最多であった.(2) 岩峰のブナは主にミズナラ、ホオノキ、シラカンバと混生し、競合する針葉樹は記録されなかった.(3) 植物群落の種構成は日本海側に成立するブナ林に類似していた.(4) 土壌pHはやや酸性で5.4~5.5であり、無機態窒素は全国のブナ林の値と大きな違いはなかった.以上の知見から、礼文華峠の岩峰上のブナ個体群は、その生育に適した気候条件に加え、本州の岩峰などでしばし

ば優占する針葉樹類が不在であるなどの条件が重 なって成立したと考えられた.

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