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A Comparative Study of the Vegetation Structure of the *Fagus orientalis* Forests in Iran and the *Fagus crenata* Forests in Japan

アキバリニア　モスレム*・福嶋　司**・上條隆志**：

イランのオリエントブナ林と日本のブナ林の植生構造の比較

Abstract

The vegetation structures of *Fagus orientalis* forests in Iran and *F. crenata* forests at Tambara, Japan, were compared. On the physiognomy and the biomass structure, two types were observed in the Iranian beech forests. Type 1 had a tree layer of 10—20 m in height, with a dense cover of a deciduous shrub (*Vaccinium arctostaphylos*). Type 2 had two tree layers : an upper layer (30—50 m), and a lower layer (12—22 m). At Tambara, there was only one tree layer (10—20 m), with a dense cover of evergreen shrubs (*Sasa* spp.). On the life form structure, the beech forests in Iran were rich in hemicryptophytes, while those at Tambara were rich in phanerophytes. Phytosociologically, the beech forests in Iran came under two associations ; the Arctostaphylo-Fagetum association (Type 1), and the Rusco-Fagetum association (Type 2) with three subassociations. The beech forests at Tambara came under the Saso kurilensis-Fagetum crenatae association with two subassociations. In both the beech forests of Iran and Tambara, Ericaceae were found only on the drier sites, and ferns on the wetter sites. The relationships between edaphical condition and floristic composition were similar in both countries.

Key words : *Fagus crenata, Fagus orientalis,* Iran, phytosociological comparison, vegetation structure.

During the last 50 years, there has been a 40% decrease in forest area in Iran ; a number of Iranian beech (*Fagus orientalis*) forests have been destroyed. As regards the regeneration of Iranian beech forests, Akbarinia and Hukusima (1995) reported the regeneration process after cutting. However, no detailed phytosociological analysis has previously been carried out. Therefore it has become especially urgent to describe in detail floristic composition and regeneration of Iranian beech forests. On the other hand, in Japan, *Fagus crenata* forests have been analyzed using a phytosociological approach (Sasaki 1964 ; Hukusima 1982 ; Hukusima and Kershaw 1988 ; Miyawaki 1981, 1982, 1986 ; Takeda and Ikuta 1986 ; Hukusima *et al.* 1994, 1995 etc.), and a regeneration approach (Nakashizuka and Numata 1982 ; Yamamoto 1989 ; Akbarinia *et al.* 1993 ; Kogasaka *et al.* 1993 etc.). These studies provide a useful basis of comparison between Iranian beech forests and Japanese beech forests. In this study, as part of an overall comparison of the beech forests in Iran and in Japan, we analyzed the vegetation structure of the *Fagus orientalis* forests on the Arborz mountains in Iran and the *Fagus crenata* forests at Tambara, Japan. The beech forests at Tambara have been studied by the same authors (Akbarinia *et al.* 1993 ; Kogasaka *et al.* 1993 ; Hukusima *et al.* 1994), therefore the vegetation data collected there could be used in the comparative study. Biomass structure, vegetation

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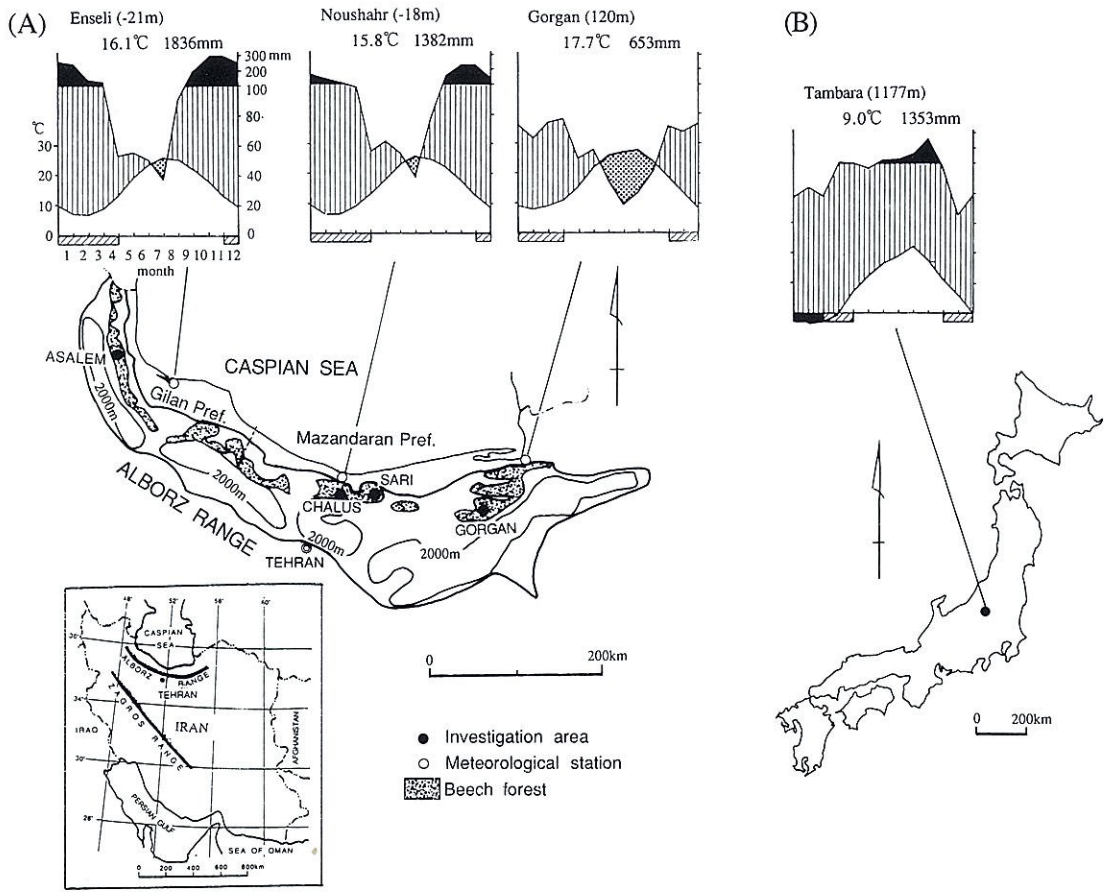

Fig. 1. Study areas： (A) climatic diagram of some locations on the Caspian Sea side, and four areas on the northern slopes of the Alborz range in Iran； (B) the same features at Tambara, Japan. In the climatic graphs, higher solid areas show months with precipitation above 100 mm, vertically hatched areas show humidity, lower solid areas show the cold season and dotted areas show the relative drought season. Numbers above the climatic graphs are the mean annual temperature and the mean annual precipitation.

physiognomy, life form structure and floristic structure were analyzed in Iran and at Tambara, based on the approaches of Mueller-Dombois and Ellenberg (1974).

Investigation Areas

The Iranian beech (*Fagus orientalis*) is distributed along a 600 km extension of the Caspian Sea coast on the Alborz mountains in Iran (Fig. 1 A). The climax beech forests are found from 900 m up to 1800 m a.s.l. in Gilan Prefecture, and from 900 m up to 2200 m a.s.l. in central Mazandaran Prefecture. Four sites, Chalus, Sari and Gorgan in Mazandaran Pref., and Asalem in Gilan Pref., were chosen for this study. We also studied the Japanese beech (*Fagus crenata*) forests at Tambara highland in Gunma Prefecture in central Honshu (Fig. 1 B). The climax beech forests are found from 1000 m up to 1500 m a.s.l. Figure 1 shows climatic conditions using the technique of Walter *et al.* (1975). The distribution of rainfall is comparatively different between the two sites. The Tambara site is wet during the whole year, while in Iran, rainfall is higher in the west, but lower in the east and is characterized by a drought season.

Method

The present study follows the methodology of Braun-Blanquet (1964). Forty-six stands in the four beech forests from the western part of Gilan Prefecture to the eastern part of Mazandaran

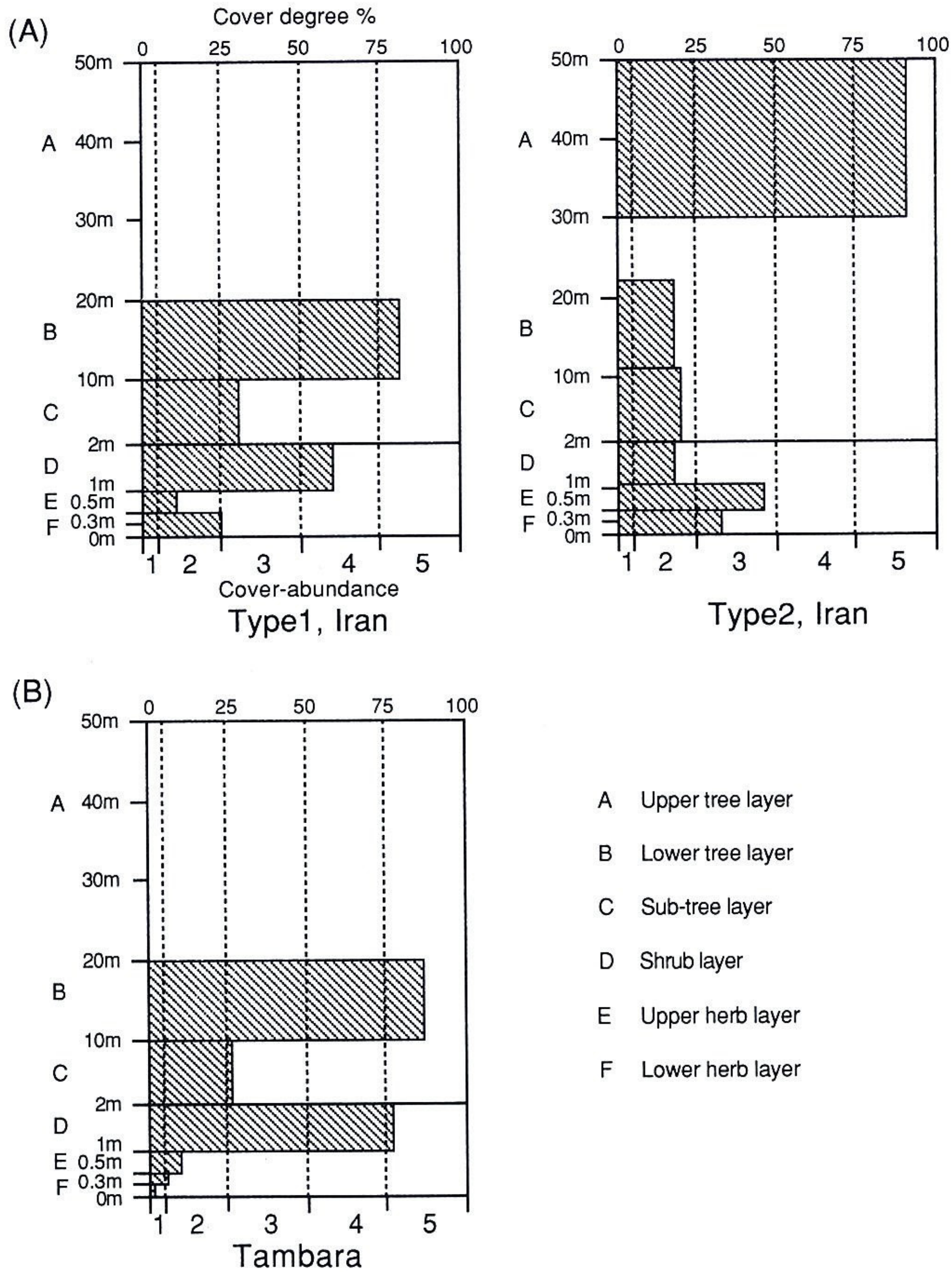

Fig. 2. Layer diagrams of (A) *Fagus orientalis* forests (Type 1, average of 7 stands, and Type 2, average of 39 stands) in Iran, and (B) *Fagus crenata* forests (average of 41 stands) at Tambara, Japan.

Prefecture in Iran, and 41 stands were selected at Tambara, Japan. Phytosociological data were treated following Ellenberg (1956) and summarized into synthesis tables by tabular comparison.

Results

Vegetation physiognomy and biomass structure

On the vegetation physiognomy, two types of beech forest were found in Iran. Type 1 was characterized by having low tree heights (10—20

m) with a dense shrub cover, while Type 2 had tall trees, 30—50 m in height, and no shrub cover. At Tambara, the *Fagus crenata* trees formed a dense, rounded canopy with a height of 10—20 m. The well-developed dense shrub layer was characterized by three *Sasa* spp. Biomass structure is related to the spacing and the height of plants forming the matrix of the vegetation cover in each layer (Mueller-Dombois and Ellenberg 1974). Figure 2 shows the layer diagram of the two types of Iranian beech forests and the beech forest at Tambara.

In Iran, the Type 1 forests were dominated by a tree layer of *Fagus orientalis* with a 70% to 85% cover, while the subtree layer had a lower cover (30%). Due to the presence of *Vaccinium arctostaphylos* the shrub layer in the Type 1 was higher in cover (60%) than the Type 2, which had no shrub species, but was characterized by a low cover of tree saplings. The Type 2 forests, with tree species such as *F. orientalis, Carpinus betulus, Acer velutinum, A. laetum, Quercus castaneifolia, Ulmus glabra, Tilia begoniifolia* and *Fraxinus coriarica,* had a cover of more than 85% in the upper layer. Species such as *Sorbus torminalis, Crataegus ambigua, Mespilus germanica, Prunus caspica* and *P. avium* had a 15% cover in the lower layer. The subtree and shrub layers had a very low cover of 20% and 15%, respectively, while the herb layer had a high cover of 45%.

At Tambara, the dominant species, *F. crenata,* was accompanied by *Aesculus turbinata* and *Magnolia obovata,* which together comprised a cover of more than 85%. The subtree layer, with a cover of more than 25%, contained *Acer japonicum,* and *A. palmatum* var. *matsumurae.* The shrub layer was dominated by *Sasa* spp., namely *Sasa kurilensis, S. senanensis* and *S. palmatum,* with other well developed evergreen shrubs including *Ilex crenata* var. *paludosa* and *I. leucoclada.* These shrubs had a cover of more than 75%. The herb layer comprised of many species including *Peracarpa carnosa* var. *circaeoides, Trilium smallii* and *Rubus pectinellus.* At 15% the cover of this layer was lower than that of the shrub layer.

Life form structure

The life forms of all the plant species in beech forests of both countries were determined using Raunkiaer life form (Raunkiaer 1934) with revised subdivision from Ellenberg and Mueller-Dombois (1967), and then further subdivided by Suzuki and Arakane (1968). Applying the Raunkiaer life form, the predominant vascular plants were hemicryptophytes in the Iranian beech forests with 61% distribution, while the other life forms had a comparatively lower percentage distribution (Table 1). Therophytes were present only in the Iranian beech forests. At Tambara, nanophanerophytes had the highest percentage distribution of all life forms (33%), and phanerophytes and hemicryptophytes had 31% and 20% distributions, respectively. Using the approach of Suzuki and Arakane (1968), scapose hemicryptophytes (HSC) had the highest presence (45 species) in Iran, followed by the deciduous broad-leaved trees (DML) with 16 species (Table 1). At Tambara, the 32 species of deciduous broad-leaved trees (DML) had the highest number of species among all life forms, this was followed by deciduous broad-leaved shrubs (DNL).

Floristic structure

The Iranian beech forests were composed of 52 families, 85 genera and 106 species (Table 2). There were 26 families (50%), and 16 genera (19%), with taxa common to the beech forests at Tambara, but no common species. Phytosociologically, the Iranian beech forests were identified as two associations (Table 3): Arctostaphylo-Fagetum (Habibi 1984) and Rusco-Fagetum (Habibi 1984). The Arctostaphylo-Fagetum association was distributed on acidic soils on dry ridges in a small part of Gilan Prefecture. Four character species were identified including *Vaccinium arctostaphylos* which was the calcifugous species with the highest cover. The Type 1 beech forests belonged to this association. The Rusco-Fagetum association was distributed on calcareous soils in a broad area of the Alborz mountains with 6 widely distributed character species. The Type 2 beech forests belonged to this association. The Rusco-Fagetum association was subdivided into the following three subassociations (Table 3): Typicum (Ⅱ-A), Luzuletosum (Ⅱ-B) and Matteuccietosum (Ⅱ-C). The Typical subassociation was found in drier climates, espe-

Table 1. Raunkiaer life forms (1934) and revised subdivision from Suzuki and Arakane (1968). Number of species in each life form of *Fagus orientalis* forests in Iran and *Fagus crenata* forests at Tambara, Japan

Raunkiaer life form	Suzuki & Arakane life form	Symbol	Number of species Iran	Tambara
	Evergreen broad-leaved tree	EML	0	0
Phanerophyte (P)	Deciduous broad-leaved tree	DML	16	32
	Evergreen needle-leaved tree	EMA	0	1
	Evergreen needle-leaved shrub	ENA	0	1
	Evergreen broad-leaved shrub	ENL	2	5
	Deciduous broad-leaved shrub	DNL	2	15
	Semi-evergreen broad-leaved shrub	SNL	0	0
Nanophanerophyte (NP)	Semi-evergreen graminoid leaved shrub	SNG	0	0
	Evergreen graminoid leaved shrub	ENG	0	3
	Evergreen liana	EL	1	2
	Deciduous liana	DL	1	9
	Semi-evergreen liana	SL	1	0
	Reptant chamaephyte	CHR	0	0
Chamaephyte (CH)	Frutescent chamaephyte	CHF	0	1
	Sclerophyllous chamaephyte	CHS	0	0
	Herbaceous chamaephyte	CHV	0	1
	Scapose hemicryptophyte	HSC	45	7
Hemicryptophyte (H)	Climber hemicryptophyte	HSD	2	1
	Caespitose hemicryptophyte	HC	8	3
	Rosette hemicryptophyte	HR	10	10
	Rhizome-geophyte	GR	10	11
Geophyte (G)	Root-budding geophyte	GRD	1	1
	Bulbose geophyte	GB	2	1
	Parasite geophyte	GP	1	1
Therophyte (TH)	Therophyte	TH	3	0
Epiphyte (E)	Epiphyte	E	1	1
Total			106	106

Table 2. Number of families, genera and species of *Fagus orientalis* forests in Iran and *Fagus crenata* forests at Tambara, Japan, and their common taxa

	Family	Genus	Species
Iran	52	85	106
Japan (Tambara)	48	72	106
Common taxa	26	16	0

cially at the highest altitude in Mazandaran Prefecture. The Luzuletosum subassociation had three variants: the Typical variant (II–B–a) was distributed mainly on the flat sites in the central part of the Arborz mountains from 1300 m up to 1500 m a.s.l.; the *Tilia begoniifolia* variant (II–B–b) was present mainly on the steep northeastern slopes in Gilan Prefecture; the *Festuca ovina* variant (II–B–c) was distributed both to the west of Gilan at low altitude (650–820 m a.s.l.), and to the east of Mazandaran at high altitude (above 1900 m a.s.l.). In the distribution areas of this variant in Gilan, and only on the southeastern slopes, *Quercus castaneifolia* and *Fagus orientalis* were always co-dominant species. The Matteuccietosum subassociation was found only on the wetter sites in Gilan Prefecture. Here *Matteuccia struthiopteris*, along with *Athyrium filix-femina* and *Dryopteris filix-mas*, were the dominant species of the forest floor.

The beech forests at Tambara were identified as an association of Saso kurilensis-Fagetum crenatae (Suzuki 1949). This was subdivided into two subassociations (Table 4): Aesculetosum (I–A) and Typicum (I–B). The Aesculetosum

Table 3. Sythesis table of *Fagus orientalis* forests in Iran

I　Arctostaphylo-Fagetum association
II　Rusco-Fagetum association
　A　Typical subassociation
　B　Luzuletosum subassociation
　　a　Typical variant
　　b　*Tilia begoniifolia* variant
　　c　*Festuca ovina* variant
　C　Matteuccietosum subassociation

Life form	Species name	I	II				
	Subassociation		A	B			C
	Variant			a	b	c	
	Number of stands	7	7	10	14	4	4
	Average of component species	26	19	29	28	28	29
Character species of Arctostaphylo-Fagetum							
DNL	*Vaccinium arctostaphylos*	V	·	·	·	·	·
E	*Polypodium vulgare*	V	·	·	+	·	·
HSC	Umbelliferae sp.	III	·	·	·	·	·
GR	*Petasites officinalis*	III	·	·	·	·	·
DML	*Sorbus aucuparia*	III	·	·	·	·	·
Character species of Rusco-Fagetum							
DML	*Acer velutinum*	I	III	V	V	2	1
HSC	*Solanum kieseritzkii*	·	II	V	V	3	3
GR	*Athyrium filix-femina*	I	III	I	V	·	4
DML	*Ulmus glabra*	·	I	V	II	4	·
HSC	*Euphorbia amygdaloides*	I	III	IV	I	·	3
DML	*Quercus castaneifolia*	·	III	II	I	4	·
Differential species of Luzuletosum							
SL	*Rubus prsicus*	III	·	IV	V	4	4
HC	*Festuca drymeia*	IV	·	II	V	2	3
HSC	*Sanicula europaea*	I	·	IV	IV	·	2
HR	*Luzula forestri*	III	·	V	II	3	·
EL	*Hedera helix*	I	·	II	IV	3	·
DML	*Prunus avium*	·	·	III	II	1	·
HSC	*Epimedium pinattum*	·	·	+	II	3	·
HSC	*Vincetoxicum nigrum*	·	·	III	II	·	·
Differential species of *Tillia begoniifolia* variant							
DML	*Tilia begoniifolia*	I	·	·	V	·	·
HR	*Polystichum setiferum*	III	·	·	III	·	1
HSC	*Campanula persicifolia*	III	·	·	III	·	·
Differential species of *Festuca ovina* variant							
DML	*Crataegus ambigua*	·	III	·	·	3	·
HC	*Festuca ovina*	·	III	·	·	3	·
HC	*Dactyilis glomerata*	·	·	·	·	3	·
HSC	*Lathyrus pratensis*	·	·	·	·	3	·
Differential species of Matteuccietosum							
GR	*Matteuccia struthiopteris*	·	·	·	·	·	4
TH	*Impatiens noli-tangere*	·	·	·	·	·	4
GR	*Petasites albus*	·	·	·	·	·	3
Character species of higher rank of vegetation units and companions							
DML	*Fagus orientalis*	V	V	V	V	4	4
DML	*Carpinus betulus*	IV	V	V	V	3	2
HSC	*Galium odoratum*	V	V	V	V	·	4
HR	*Viola odorata*	V	IV	V	V	3	3
HC	*Carex maximum*	V	III	V	V	4	2
HSD	*Vicia cracca*	V	IV	IV	V	2	3
HC	*Hypericum androsaemum*	IV	I	IV	V	4	4
HSC	*Salvia glutinosa*	IV	IV	III	IV	·	4
DML	*Acer laetum*	III	I	IV	V	4	2
HR	*Dryopteris filix-mas*	III	III	IV	IV	+	4
HSC	*Stachys sylvatica*	II	V	II	IV	4	1
GR	*Epipactis* cf. *leptochila*	I	III	IV	III	2	3
HSC	*Arabis hirsuta*	V	V	+	IV	·	3
HSC	*Fragaria vesca*	III	I	V	III	1	3
HR	*Primula heterochroma*	II	I	+	V	4	·
HSC	*Geranium robertianum*	I	III	II	III	2	4
DML	*Sorbus torminalis*	V	I	II	II	4	1
TH	*Poa bulbosa*	IV	III	III	II	·	·
HSC	*Lathyrus vernus*	II	III	II	III	2	·
HR	*Viola sylvatica*	I	I	III	II	2	·
GR	*Polygonatum orientale*	II	III	·	II	·	3
HSC	*Geranium sylvaticum*	·	·	·	II	·	4
HSC	*Asperula odorata*	V	I	II	+	·	·
DML	*Euonymus velutina*	IV	III	·	+	·	·
DML	*Prunus caspica*	·	III	III	+	·	·
ENL	*Rhuscus hyrcanum*	I	III	·	II	·	·
HSC	*Nepeta cataria*	III	·	·	I	·	4
HSC	*Arenaria marginata*	IV	·	·	+	·	2
HSC	*Solidago virgaurea*	II	·	·	II	2	·
HSD	*Cynanchum vincetoxicum*	·	·	·	II	3	·
TH	*Poa annua*	·	I	·	II	2	·
HSC	*Saussurea alpina*	I	·	·	II	1	·
HSC	*Circaea lutetiana*	I	·	·	I	1	3
HSC	*Epilobium hirsutum*	II	·	·	·	·	2
DNL	*Daphne angustifolia*	III	I	·	II	·	·
DML	*Mespilus germanica*	·	I	+	·	4	·
GB	*Orchis palustris*	·	III	·	+	·	·
HSC	*Prunella vulgaris*	·	·	·	·	1	·
DML	*Alnus subcordata*	·	·	·	·	1	·
GB	*Tamus communis*	·	III	·	·	·	·
HR	*Asplenium trichomanes*	III	·	·	I	·	·
HSC	*Urtica dioica*	·	I	·	+	1	2
HR	*Phyllitis scoloropendrium*	·	I	·	II	·	·
HSC	*Lamium album*	·	·	II	·	·	·
HSC	*Cirsium oleraceum*	I	I	·	·	1	·
HSC	*Ixeris stolonifera*	II	·	·	+	·	·
HC	Gramineae sp.	·	·	·	+	2	·
HC	*Carex sylvatica*	·	·	+	·	1	·
HSC	*Saussurea alpina* v. *macrophylla*	·	·	·	+	1	·
HC	*Hordeum vulgare*	I	·	+	·	·	·
HSC	*Salvia pratensis*	·	·	·	I	·	·
GP	*Orobanche minor*	I	·	·	+	·	·
HSC	*Sedum stoloniferum*	I	·	·	·	·	1
HSC	*Mercurialis perennis*	·	·	·	I	·	1
HSC	*Atropa belladonna*	·	·	I	+	·	·
DML	*Fraxinus coriarica*	·	·	·	+	2	·
HSC	*Actinostemma* sp.	·	·	·	II	·	·
HSC	*Rumex nepalensis*	·	·	·	·	1	·
HSC	*Pilea fontana*	·	·	·	+	·	·
GR	*Epipogium aphyllum*	·	·	+	·	·	·
ENL	*Ilex hyrcana*	·	·	+	·	·	·
HSC	*Centaurea* sp.	·	·	·	+	·	·
HR	*Asplenium adiantum*	·	·	·	+	·	·
HSC	*Cirsium lanceolatum*	·	·	·	+	·	·
HSC	*Lanthyrus montanus*	·	·	·	+	·	·
HSC	*Ranunculus arvensis*	·	I	·	·	·	·
HC	*Avena fatua*	·	·	·	·	·	1
HSC	*Scrophularia nodosa*	I	·	·	·	·	·
GR	*Thelyptris palustris*	I	·	·	·	·	·
HSC	*Malva rotundifolia*	I	·	·	·	·	·
GRD	*Paeonia corallina*	I	·	·	·	·	·
HSC	*Arabis caucasica*	I	·	·	·	·	·
GR	*Pyrola secunda*	I	·	·	·	·	·
HSC	*Trifolium pratense*	·	·	·	·	1	·
GB	*Cyclamen elegans*	·	·	·	+	·	·
HSC	*Bupleurum falcatum*	·	·	·	·	·	+
GR	*Pyrola rotundifolia*	·	·	·	·	·	+

Table 4. Synthesis table of *Fagus crenata* forests at Tambara, Japan

I Saso kurilensis-Fagetum crenatae association
  A Aesculetosum subassociation
    a Typical variant
    b *Viburnum furcatum* variant
  B Typical subassociation
    a Typical variant
    b *Thujopsis dolabrata* variant

Association		I			
Subassociation		A		B	
Variant		a	b	a	b
Number of stands		17	9	4	11
Average of component species		24	31	27	34
Life form	Species name				
Differential species of Aesculetosum					
DML	*Aesculus turbinata*	V	IV	·	I
HR	*Dryopteris crassirhizoma*	V	IV	·	·
DML	*Acer nipponicum*	V	III	·	·
HSC	*Peracarpa carnosa* v. *circaeoides*	V	III	·	·
GR	*Trillium smallii*	IV	I	·	+
HSC	*Stellaria diversiflora*	III	II	·	·
HSC	*Galium trifloriforme*	III	II	·	·
GR	*Diplazium squamigerum*	III	II	·	·
DML	*Sambucus sieboldiana*	III	I	·	·
DNL	*Hydrangea macrophylla* v. *megacarpa*	III	·	·	·
DNL	*Rubus pectinellus*	III	·	·	·
Differential species of *Viburnum furcatum* variant					
DML	*Viburnum furcatum*	·	V	4	V
HR	*Arachniodes mutica*	·	III	4	V
ENL	*Ilex crenata* v. *paludosa*	+	IV	2	V
DML	*Rhus trichocarpa*	·	III	3	V
EML	*Daphniphyllum macropodum* v. *humile*	·	III	2	IV
DML	*Hydrangea paniculata*	·	III	2	III
DML	*Acer sieboldianum*	·	II	3	III
HC	*Carex morrowii* v. *temnolepis*	·	II	1	III
DML	*Acer micranthum*	·	III	·	II
Differential species of *Thujopsis dolabrata* variant					
EMA	*Thujopsis dolabrata*	·	II	·	V
CHF	*Lycopodium serratum*	·	I	·	IV
DNL	*Viburnum urceolatum* v. *procumbens*	·	I	·	IV
DNL	*Leucothoe grayana* v. *oblongifolia*	·	·	·	IV
ENL	*Ilex sugerokii* v. *brevipedunculata*	·	·	·	IV
DNL	*Vaccinium hirtum*	·	·	·	III
EL	*Mitchella undulata*	·	·	·	III
ENG	*Sasa senanensis*	III	IV	·	III
DNL	*Euonymus macropterus*	II	II	·	II
DNL	*Ligustrum tschonoskii*	IV	IV	·	II
DML	*Acer mono* v. *mayrii*	IV	IV	·	IV
DNL	*Rhododendron albrechtii*	·	·	·	III
Character species of association and higher rank of vegetation units and companions					
HC	*Carex dolichostachya* v. *glaberrima*	V	V	2	I
HR	*Dryopteris expansa*	IV	IV	1	+
ENA	*Cephalotaxus harringtonia* v. *nana*	III	V	2	+
DL	*Schizophragma hydrangeoides*	II	IV	3	+
ENG	*Sasa palmata*	III	II	2	·
DML	*Acer japonicum*	III	V	3	V
ENL	*Skimmia japonica* v. *intermedia* f. *repens*	I	V	4	V
ENL	*Ilex leucoclada*	I	V	4	V
DML	*Fraxinus lanuginosa*	II	IV	4	V
DML	*Magnolia salicifolia*	II	III	3	V
DML	*Prunus grayana*	I	IV	2	IV
DML	*Clethra barbinervis*	I	I	3	IV
DML	*Acer rufinerve*	+	III	2	IV
DL	*Tripterygium regelii*	+	III	1	III
DML	*Fagus crenata*	V	V	4	V
DNL	*Lindera umbellata* v. *membranacea*	V	V	4	V
DL	*Rhus ambigua*	V	V	4	V
ENG	*Sasa kurilensis*	V	V	4	V
DML	*Acanthopanax sciadophylloides*	VI	V	4	V
DL	*Hydrangea petiolaris*	VI	V	3	III
DML	*Acer palmatum* v. *matsumurae*	VI	III	2	III
GP	*Monotropastrum globosum*	III	II	1	III
DML	*Magnolia obovata*	I	III	3	III
HR	*Struthiopteris nipponica*	+	I	1	III
DML	*Pterocarya rhoifolia*	I	I	1	I
DNL	*Euonymus alatus* f. *ciliato-dentatus*	I	I	1	II
DML	*Tilia japonica*	+	I	·	+
DL	*Actinidia arguta*	I	I	·	+
DL	*Celastrus orbiculatus*	I	I	·	II
GR	*Paris tetraphylla*	I	II	·	I
GR	*Smilacina hondoensis*	II	I	·	+
DML	*Acer argutum*	II	II	1	·
DNL	*Euonymus oxyphyllus*	II	II	·	+
DML	*Kalopanax pictus*	·	I	1	+
DML	*Corylus sieboldiana*	·	I	1	II
HR	*Arachniodes standishii*	+	I	·	·
DML	*Phellodendron amurense*	+	I	·	·
DNL	*Ilex geniculata* v. *glabra*	+	·	·	+
HSC	*Panax japonicus*	I	I	·	·
DML	*Betula ermanii*	·	I	·	+
HR	*Osmunda cinnamomea* v. *fokiensis*	·	I	·	II
GRD	*Asarum sieboldii*	·	II	2	·
DML	*Quercus mongolica* v. *crispula*	·	·	1	I
DNL	*Viburnum wrightii*	·	·	1	I
DML	*Sorbus alnifolia*	·	·	1	III
DNL	*Vaccinium japonicum*	·	·	1	III
HC	*Carex foliosissima*	II	II	1	·
DML	*Sorbus commixta*	·	I	1	III
HR	*Plagiogyria matsumureana*	·	I	2	III
HSD	*Tripterospermum japonicum*	·	I	1	III
HR	*Dryopteris sabaei*	·	·	2	+
E	*Lepisorus ussuriensis* v. *distans*	+	·	·	·
GB	*Arisaema robustum*	+	·	·	·
GR	*Leptogramma mollissima*	+	·	·	·
DML	*Cornus controversa*	+	·	·	·
DL	*Clematis japonica*	+	·	·	·
GR	*Smilacina japonica*	+	·	·	·
HSC	*Laportea bulbifera*	+	·	·	·
HR	*Polystichum tripteron*	+	·	·	·
HSC	*Polygonum cuspidatum*	I	·	·	·
DL	*Vitis coignetiae*	I	·	·	·
GR	*Maianthemum dilatatum*	·	I	·	·
GR	*Smilacina yesoensis*	·	I	·	·
HSC	*Galium japonicum*	·	I	·	·
GR	*Streptopus streptopoides* v. *japonicus*	·	I	·	·
DML	*Symplocos sawafutagi*	·	I	·	·
DML	*Fraxinus mandshurica* v. *japonica*	·	·	1	·
DML	*Acer diabolicum*	·	·	1	·
GR	*Athyrium yokoscense*	·	·	2	·
DL	*Smilax sieboldii*	·	·	·	+
HR	*Osmunda japonica*	·	·	·	+
DNL	*Daphne kamtschatica* v. *jezoensis*	·	·	·	+
GR	*Pyrola japonica*	·	·	·	+
HR	*Hosta albo-marginata*	·	·	·	+
CHV	*Lycopodium obscurum*	·	·	·	+
DNL	*Tripetaleia paniculata*	·	·	·	I

subassociation was found on the wetter sites. The differential species of this subassociation contained two fern species, *Dryopteris crassirhizoma* and *Diplazium squamigerum*. Aesculetosum subassociation had two variants as follows : the Typical variant (I -A-a) was found on the flat summit areas, while the *Viburnum furcatum* variant (I -A-b) was found on the gentle slopes. The Typical subassociation also had two variants : the Typical variant (I -B-a) was distributed mainly on the middle part of the slopes ; the *Thujopsis dolabrata* variant (I -B-b), with some dry indicator species (*Rhododendron albrechtii, Euonymus macropterus, Vaccinium hirtum*), was distributed on the ridge and the convex site around the moor.

Discussion

Physiognomically, the Iranian beech forests were composed of the two types. The Arctostaphylo-Fagetum association (Type 1) had low tree height (20 m), with similar physiognomy and biomass structure to the beech forests at Tambara. The Rusco-Fagetum association (Type 2) had trees above 40 m in height. The Iranian beech forests, studied by Akbarinia and Hukusima (1995) in terms of regeneration process, belong to Type 2. According to Peters (1992), European beech (*Fagus sylvatica*) forests and American beech (*Fagus grandifolia*) forests have tall trees, 34—42 m and 35—40 m in height, respectively. The Type 2 forests seem to be similar to these European and American beech forests. Most areas of beech forest in Iran belong to Type 2, with a very thin cover of shrubs and a thick cover of herbs. The comparatively lower abundance of herbs in Type 1, and in the beech forests at Tambara, may be the result of critical light conditions under the dense shrub layer.

The percentage distribution of hemicryptophytes in the Iranian beech forests was much higher than that at Tambara (Table 1). Among hemicryptophytes, the number of species of scapose hemicryptophytes (HSC) in the Iranian beech forests was at least six times that of the beech forests at Tambara. At the highest percentage distribution of hemicryptophytes, the life form structure of the Iranian beech forests are more similar to that reported for European beech forests by Raunkiaer (1934) and Ellenberg (1988). Furthermore, evergreen graminoide leaved shrubs (ENG) such as *Sasa* do not occur in the Iranian beech forests (Table 1). The life form structure of the Iranian beech forests may be more similar to Japanese beech forests without *Sasa* reported by Sasaki (1964), Miyawaki (1981, 1982, 1986), Takeda and Ikuta (1986) and Hukusima *et al.* (1995), than those with *Sasa*.

The beech forests in Iran and those at Tambara both had the same number of species (106 species). This number indicates higher species diversity in the smaller Tambara area than in the Iranian beech forests. In addition, the beech forests at Tambara had two times as many phanerophytes as those in Iran. As regards the phanerophytes the Aceraceae had the highest number of species (8 species) at Tambara, and one species in the nanophanerophytes. According to Hotta (1974), the Aceraceae is a companion family of beech species in the Northern Hemisphere, with many species distributed in East Asia. The Iranian beech forests had only two species in this family, *Acer velutinum* and *A. laetum*. These two species are also characteristic of European beech forests (Jahn 1991).

There are many common species in the tree layer of the Iranian and European beech forests. In the tree layer, these species include *Carpinus betulus, Ulmus glabra,* and *Sorbus torminalis.* In the herb layer, common species include *Lathyrus vernus, Geranium sylvaticum, Poa bulbosa, P. annua, Euphorbia amygdaloides, Petasites albus and Impatiens noli-tangere.* Twenty two of the herb species of the Iranian beech forests are also distributed in Japan, but they are found on open areas or around paddy fields. Of these, 14 species including *Festuca ovina, Poa annua* and *Geranium robertianum* are native, and 8 species including *Dactylis glomerata* and *Trifolium pratense* were introduced to Japan (Ohwi and Kitagawa 1992 ; Nakaike 1992). *Festuca ovina* and *Poa annua* are widely distributed in the cool temperate zones of the Northern Hemisphere. In Iran, the non-existence of *Sasa* and the effect of cattle grazing may enable these common species to grow in the beech forests.

In both the beech forests of Iran and Tambara, some families were associated with beech on drier sites (Tables 3, 4). For instance, two species of Ericaceae were found in the *Thujopsis dolabrata* variant of the Typical subassociation at Tambara, and one species was found in the Arctostaphylo-Fagetum association in Iran. Also the ferns in both beech forests were present on wetter sites; two species in the Arctostaphylo-Fagetum subassociation at Tambara, and one species in the Matteuccietosum variant. Thus the relationships between edaphic condition and floristic composition in the beech forests were similar in both countries.

It can be concluded that the Iranian beech forests have strong similarities to the European beech forests in terms of the life form structure and the floristic structure. In particular, the tree heights are similar in the Type 2 beech forests and the European beech forests. The Type 1 beech forests in Iran, however, show some similarities to the beech forests at Tambara, Japan, due to the low tree heights and the presence of dense shrub cover. At Tambara and at the other beech forests of Japan, *Sasa* plays an important inhibiting role in forest regeneration of beech (Nakashizuka 1988; Akbarinia *et al.* 1993). *Vaccinium arctostaphylos* possibly has a similar effect in the Type 1 beech forests in Iran. Further studies will be necessary to ascertain the extent of an inhibiting role of this species.

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摘　要

イランのカスピ海沿岸のアルボールズ山脈に分布するオリエントブナ（*Fagus orientalis*）林の性質はまだほとんど解明されていない。本研究では、Mueller-Dombois and Ellenberg（1974）が提唱した植生構造（相観構造、バイオマス構造、生活形構造、組成構造）の解析方法を用いて、イランのブナ林と日本の群馬県玉原高原のブナ（*Fagus crenata*）林を比較した。相観構造とバイオマス構造でみると、イランのブナ林は2タイプに類型化された。タイプ1のブナ林は群落高が20 m程度で、*Vaccinium arctostaphylos*の低木層が発達し、イラン西部の酸性土壌上に分布していた。このタイプ1のブナ林は群落高、階層構造とも玉原のブナ林に類似していた。タイプ2のブナ林は群落高が40 m以上で、草本層が発達し、アルボールズ山脈に広域的に分布していた。生活形構造では、イランのブナ林はヨーロッパのブナ林と同じく半地中植物が多い（61%）のに対し、玉原のブナ林は地上植物が多かった（33%）。イランのブナ林の46調査試料と玉原のブナ林の41調査試料で、それぞれ組成表を作成して組成構造を比較した。その結果、イランのブナ林は既存の2群集（Arctostaphylo-Fagetum と Rusco-Fagetum）に同定される3亜群集、3変群

集が区分され、玉原のブナ林は既存の1群集（Saso kurilensis-Fagetum crenatae）、2亜群集に同定される4変群集が区分された。また、イランのタイプ1のブナ林はArctostaphylo-Fagetumに、タイプ2のブナ林はRusco-Fagetumに対応していた。両国のブナ林の組成は全く異なっているが、湿性立地にはシダ植物の種によって特徴づけられる下位単位が、乾性立地にはツツジ科の種によって特徴づけられる下位単位が形成されることが共通していた。

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○ 矢原徹一 **花の性—その進化を探る** A4判，316頁．1995年5月19日，東京大学出版会．3,914円．

最近，植物の繁殖に関する著作が2冊相次いで出版された。これはその中の一つである。菊沢「植物の繁殖生態学」がおもに大学院生以上を対象としているために著者の個性があまり出ていないのに対し，この本は進化生態学を志す学生にむけた教科書なのか，あるいは中堅研究者の書いた魅力あふれる今までの道のりなのか，いずれの範疇にはいるにしろ著者の個性や意見がはっきり読みとることができる。そのため読む側を思わず夢中にさせてしまう非常にユニークな本である。

その基本構成は，著者の学生時代から現在にいたるまでの研究の興味とテーマの発展に従っており，その広範な研究分野を反映し6章にわたっている。タイトル通り花の性に関する様々な繁殖生態学の問題が，著者の研究の発展に従って語られている。最初に著者の研究の出発点となったヤブマオを材料とした無性生殖の進化についての問題から始まり，ヒヨドリバナを用いて自家受粉と種分化の問題へのアプローチ，屋久島の固有種への興味から始まった自家受粉と種の進化の問題，さらにそれから発展した屋久島や秩父での虫媒花の生物学の問題，数理モデルをもちいた自家受粉の進化へのアプローチ，モデルの検証をめざしておこなったキツリフネでの閉鎖花の研究の順に章だてられている。いずれの章においても，なぜそのテーマを選んだのか，なぜその材料を選んだのか，またそのテーマは進化生態学の研究分野の中でどういう位置づけにあり，どのような研究の歴史を持つのか，さらに著者はどのような作業仮説を考えそれを証明していくために，どのように考え悩み問題を解決していったかが中心となっている。従来の教科書や総説では，さまざまな説が天下り的に淡々と述べられているのが普通である。しかしこれから勉強していこうとしている学生にとって，その結論や説が生まれるまでにどのような思考過程や失敗が隠されているかを知ることはたいへん重要である。その意味でこの本は従来の教科書には全く見られない科学の人間臭さも同時に出ているため，科学読み物としても十分におもしろくよめる本である。さらに，この章の順は一応研究の発展順になってはいるものの，要所毎にBOXの形で用語の丁寧な説明がなされており，この部分だけでも教科書としての価値を十分持つ。一方で，内容は多方面にわたる話題を取り扱っているが，植物の進化生態学の中での位置付けの説明がほしい部分がいくつかあった。とくにこの本は全編が著者の視点で貫かれているが故に，初学者のための教科書としては少し見方が偏りすぎていると思われる箇所もあった。これを避けるためにも植物の繁殖に関する全般的な概説の章を設けてあれば初学者に対してより親切であったのではないか。いずれにしろ内容的には繁殖生態学の研究者にとって参考となる内容の高いレベルのものでありながら，学部学生にも興味を抱かせ内容が容易に理解できるよい教科書となっている。

(木下栄一郎)

○ 菊沢喜八郎 **植物の繁殖生態学** 菊判，283頁．1995年10月25日，蒼樹書房．4,635円．

動物に見られる著しい繁殖行動ー雄の雌に対する求愛行動，縄張の発達，魚類などにみられる産卵のための河川回帰などーは古くから多くの注目を集め，主に記述的な方法で盛んに研究されてきた。1970年代になるといわゆる繁殖戦略の考えが導入され，それまでの動物生態学や行動学は大きな転換期を迎えた。資源は有限でありその中で生育できる個体数は決まっていて，そのような状況の中で自分の遺伝子をより多く残すことができるタイプが長い時間経過した後にそうでない者と置き変わってしまう。つまり動物にみられるさまざまな行動を繁殖成功と結び付けて解釈しようという立場である。それは極論すれば繁殖行動ばかりでなく，非繁殖個体のサケが海洋中を回遊している行動などのあらゆる行動は，来るべき繁殖とその結果としての繁殖成功を高めるための準備であると解釈することであった。

植物の場合，固着性であるが故に動物でみられるような繁殖行動は当然見られない。しかし，どの齢あるいはサイズで開花するか，どのような花をどう開花させるか，果実をどのように散布するかといった植物特有な振る舞いも，動物で展開されたと同じような考え方で説明しようとする事は，自然な展開である。実際に植物の示すさまざまな振る舞いも上記の観点から理解できることが示されはじめた。しかし筆者も述べているよう