Studies on the Limestone Vegetation in Shikoku, Japan

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I. Introduction

It is well known that rock and soil of limestone have a specific effect on vegetation and harbour a flora peculiar to itself. Many botanists have investigated the plant life on limestone from various standpoints and have already discussed it in a variety of papers and text-books.*

In Japan, scattered limestone outcrops occur throughout the country. Though considerable attentions have been paid to the flora by some taxonomists and phytogeographers,* comparatively little is known about the vegetation. So far as is known, the report on the vegetation of Otaki and Geibi-kei in northern Honshû described by YOSHII and YOSHIOKA[9] is the only statistical analysis of plant communities on limestone in Japan.

In Shikoku, widely scattered limestone areas are found. For several years, the writer's attention has been attracted to the peculiar vegetation on limestone in Shikoku, and his brief descriptions of it were already published.[4),5),7),8)] The purpose of this paper is to give a sociological description from an analytical standpoint of main plant communities on limestone outcrops in Shikoku.

For the purpose of this study, the writer visited the thirty-one localities presented in Fig. 1 and Table 1. As the result of his own investigations which were carried out there, employing more than 100 quadrats, he recognized three distinct associations in Shikoku; Orixetum japonicae, Nandineto-Cyclobalanopsidetum glaucae, and Zabelieto-Carpinetum turczaninovii. Besides, there are many stands that cannot be included in any of the above-mentioned associations. They have not been surveyed satisfactorily, and only a brief note of them is given here. A more extensive description of this study will be published elsewhere.

The writer is indebted to Prof. Sirô KITAMURA of the Kyôto University for his invaluable advice and encouragement, and Dr. Jisaburô OHWI of the National Science Museum for the identification of several difficult specimens. Thanks are also due to Mr. Kazuo MORISHITA who co-operated with the writer in the field.

II. Method of Investigation

The data for the present paper were obtained from the field work carried out from April to October in 1954. The writer set 5×5 m quadrats, and determined dominance, constancy, and fidelity of the component species of the plant communities. Dominance was interpreted as described by BRAUN-BLANQUET[1)] (partly revised by SATO[2)]). Constancy and Fidelity were followed in the sense used by BRAUN-BLANQUET[1)]. The association was determined and named from the dominant and characteristic species of the communities.

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* These references are not presented for want of space.

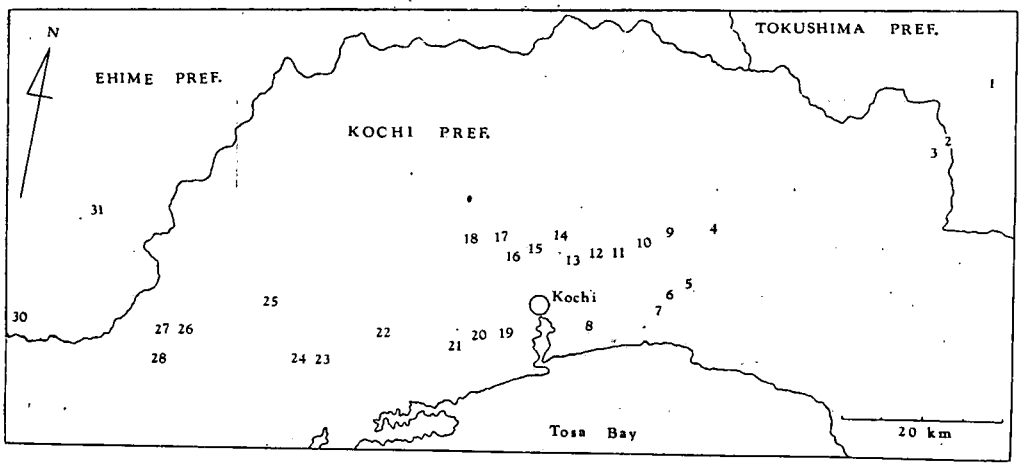

Fig. 1

Table 1

1) No.	2) Locality	Altitude (m)	3) Ass. recognized
1	Mt. Tsurugi, Mima County, Tokushima Pref.	1800—1850	3
2	Mt. Ishidate, Makiyama Village, Kami County	1100—1700	3
3	Befu, Makiyama V., Kami C.	600—1000	2,3
4	Arase, Akatsuka V., Kami C.	200— 250	2
5	Sakakawa, Sako V., Kami C.	240— 320	2
6	Shiroiwa, Sako V., Kami C.	60— 100	2
7	Mt. Sambo, Sako V., Kami C.	200— 260	2
8	Nakatani, Inabu V., Nagaoka C.	20— 100	2
9	Vicinity of Shingai Station, Nagaoka C.	160— 220	2,3
10	Wakamiya, Shingai V., Nagaoka C.	120— 200	1,2,3
11	Shirome, Kameiwa V., Nagaoka C.	130— 250	2
12	Kameiwa, Kameiwa V., Nagaoka C.	100— 150	2
13	Shirakidani, Agekura V., Nagaoka C.	320— 400	2,3
14	Shobu, Tosayama V., Tosa C.	250— 300	1
15	Hinoura, Tosayama V., Tosa C.	200— 500	1,3
16	Tsuami, Tosayama V., Tosa C.	200— 400	1,2,3
17	Kuwao-Hirose, Tosayama V., Tosa C.	120— 200	1,2,3
18	Sadanaga-Kariyama, Kagami V., Tosa C.	200— 300	1,3
19	Jigokudani, Kochi city	140— 200	2
20	Arakura Pass, Hirooka-kamino V., Agawa C.	40— 140	2
21	Kiragamine, Hirooka-kamino V., Agawa C.	200— 250	2
22	Saruta, Kusaka V., Takaoka C.	30— 100	2
23	Shimomitogi, Togano V., Takaoka C.	120— 150	2
24	Nishiyama, Ogawa V., Takaoka C.	120— 150	2,3?
25	Mt. Yokogura, Ochi Town. Takaoka C.	500— 810	2,3
26	Izumi, Choja V., Takaoka C.	600— 800	1,3
27	Mt. Torigata, Choja V., Takaoka C.	1000—1460	3
28	Yahazu Pass, Choja V., Takaoka C.	500— 780	3
29	Shirasari, Higashitsuno V., Takaoka C.	400— 600	1,3
30	Mt. Onogahara, Higashiuwa C., Ehime Pref.	1200—1400	—
31	Mimido, Kamiukena C., Ehime Pref.	350— 400	3

1). Same numbers are used throughout the map and the association tables.

2). All the localities except 1, 30, and 31 are in Kochi Prefecture. Except No. 24 (Mesozoic), all the above limestone areas belong to Palaeozoic.

3). 1 = Orixetum, 2 = Cyclobalanopsidetum, 3 = Carpinetum

III. Limestone Associations

Summarized association tables are presented on page 4 and 6—11.

(1) Orixetum japonicae.

Though the territory is usually small and scattered, this is a distict association developed on shady and moist places, often occurring along valleys and ravines. Eight stands of this association analyzed range from 140 m to 760 m above sea-level and present structures different from one another. However, *Orixa japonica* is a dominant species in the shrub layer throughout. The ococurrence of this species is not restricted to limestone but is closely connected with it.

Some association characteristics are found mixed with *Orixa japonica* in the shrub layer. Among them, *Cephalotaxus harringtonia*, *Boehmeria spicata*, *Deutzia maximowicziana*, and *Alangium platanifolium* are frequently found in this association. On the other hand, *Hosiea japonica*, which is found only in one stand, is also a good characteristic species. *Kerria japonica* is the most abundant shrub among other companions of this association.

The herb layers are mostly composed of many shade plants and are also different from one another in the floristic compositions, and constant occurrences are scarcely found. Such characteristic species as *Polystichum craspedosorum*, *Phanerophlebia* spp., *Nanocnide japonica*, *Mercurialis leiocarpa*, *Iris japonica*, etc. occur abundantly on moist places. On the contrary, *Sedum tosaense* is predominant on rather dry sites.

Sometimes, communities dominated by *Orixa japonica* are often found on other non-limestone areas and are usually developed under similar shady and moist conditions. It is a problem to be settled whether or not these communities can be included in the same association.

(2) Nandineto-Cyclobalanopsidetum glaucae.

This is commonly found in the evergreen broad-leaved forest region below altitudes of about 500 m above sea-level. Mountainsides of the above-mentioned areas are often covered with this community.

The typical stand of this association consists of three well-developed layers. The lower tree layer is dominated by evergreen oak, *Cyclobalanopsis glauca*. Though the growth of this oak is fairly good in the climatic climax forests developed on non-limestone areas, this species is usually a smaller tree or sometimes of shrub height and never a large tree on limestone. Therefore physiognomies of this community often resemble those of the so-called "Maquis" or "Garigue". Among many species associated with *Cyclobalanopsis glauca* in the lower tree layer, *Eriobotrya japonica*, *Melia azedarach* var. *japonica*, and *Xylosma japonicum* are the characteristic species of this association.

The frequent occurrence of *Nandina domestica* in the shrub layer is the most characteristic feature of this association. This species is considered as a typical calcicolous plant and is closely connected with this community especially. *Kerria japonica* is a luxuriant companion in this shrub layer.

The herb layer is usually constituted by *Onychium japonicum*, *Cyclosorus acuminatus*, *Clematis williamsii*, *Rubus buergeri*, *Ardisia japonica*, *Oplismenus undulatifolius* var. *japonicus*, *Carex sendaica* var. *nakiri*, *Liliope platyphylla*, *Ophiopogon japonicus*,

Table 2. Orixetum japonicae

Locality	14	16	16	17	18	26	29	29	Constancy	Fidelity
Altitude	250	210	220	140	200	760	510	510		
Exposition	S35W	W	W	N	S60W	S65E	N15E	S50W		
Steepness	20	5	10	25	30	25	20	30		
2nd tree & Shrub layer										
Orixa japonica	5(1)	3(1)	3(1)	5(1)	5(3)	3(2)	4(2)	5(1)	V	5
Cephalotaxus harringtonia	+(+)	2(+)	+(+)	+(+)	(+)	1(+)	−	2(+)	V	3
Kerria japonica	2(1)	3	3(+)	2(+)	+	2(+)	−	(+)	V	2
Alangium platanifolium	1	2(+)	2(+)	1(1)	−	3	2(+)	−	IV	5
Boehmeria japonica	3(+)	−	3(−)	+	−	2(+)	2(+)	−	IV	3
Euonymus fortunei v. *radicans*	−	3(1)	+	(2)	−	−	−	(+)	III	2
Ligustrum obtusifolium	+(+)	2	−	−	1(+)	+	−	−	III	2
Helwingia japonica v. *parvifolia*	(+)	2	−	(+)	−	+(+)	−	−	III	2
Torreya nucifera	−	−	+(+)	−	−	(+)	(+)	(+)	III	1
Euptela polyandra	1	−	−	5(+)	−	1	−	−	II	2
Deutzia maximowicziana	−	1	3	−	−	2(+)	−	−	II	4
Sambucus sieboldiana	−	2	−	−	−	−	−	+	II	3
Platycrater arguta	+	−	2	+	−	−	−	−	II	3
Hosiea japonica	−	−	−	−	−	3(2)	−	−	I	4
44 other species										
Herb layer										
Phanerophlebia fortunei	3	1	−	1	+	−	−	1	IV	3
Ophiopogon japonicus	1	−	+	2	−	+	2	1	IV	2
Reynoutria japonica	+	1	−	−	+	+	−	+	IV	2
Hedera rhombea	−	−	−	−	2	+	+	1	III	2
Chrysanthemum indicum	−	−	−	+	+	+	−	+	III	2
Nanocnide japonica	−	2	−	−	2	−	−	2	II	3
Rubus hakonensis	2	−	−	1	−	−	−	2	II	3
Phanerophlebia fortunei v. *clivicola*	2	−	−	1	−	−	2	−	II	3
Iris japonica	3	2	−	−	−	−	−	−	II	3
Mercurialis leiocarpa	−	−	−	+	3	1	−	−	II	3
Lycoris sanguinea	−	+	−	−	−	1	1	−	II	3
Microsorim ensatum	3	−	−	−	−	−	−	−	I	2
Polystichum craspedosorum	−	−	−	3	−	−	−	−	I	3
Sedum tosaense	−	−	3	−	−	−	−	−	I	3
Phanerophlebia yamamotoi	1	−	−	−	−	−	−	−	I	4
Polystichum mayebarae	−	−	−	−	−	−	+	−	I	3
Arabis flagellosa	−	−	−	−	−	−	−	+	I	4
54 other species										

( ) = Dominance of the same species in the herb layer.

Cymbidium virescens, etc. But, *Selaginella pachystachys* is often prominent on dry outcrops. *Carex makinoensis* is not frequent but sometimes is dominant

Probably, the characteristic combination of stunted *Cyclobalanopsis glauca* and *Nandina domestica* is essential to this association. It can be stated that this is a distinct and quite different limestone association from other *Cyclobalanopsis* communities to be found on other kinds of rock.

(3) Zabelieto-Carpinetum turczaninovii.

It is usually observed that outcrops of ridges or sunny mountainsides are occupied by this community. This is developed on such infertile limestone areas ranging from the evergreen broad-leaved to the deciduous broad- leaved climax forest region and is very remarkable against the neighbouring cnmmunities.

Carpinus turczaninovii is dominant in this community and often attains height up to 6−7 m on rather stable sites of mountainsides. But it is very stunted on ridges and

is only 1.5–2 m high. Therefore this community consists of two or three synusiae.

The lower tree and the shrub layers are composed of many characteristic species, such as *Carpinus turczaninovii*, *Spiraea nervosa*, *Rosa lusiae* var. *onoei*, *Euonymus alatus* var. *rotundatus*, *Zabelia integrifolia*, *Torreya nucifera*, etc., and companions, such as *Kerria japonica*, *Lespedeza buergeri*, *Fraxinus sieboldiana* var. *serrata*, etc. Though the occurrences of *Sabina chinensis*, *Vitis yokogurana*, *Rhamnus yoshinoi*, and *Smilax stans* are very scarce or local, they are also the characteristics of this association.

Many herbaceous plants are growing in the forest-floor. However, this floor is mostly dominated by the plants belonging to *Carex* and Graminae, and some of them are the characteristics of this association. Besides, a large number of the characteristic species, such as *Amesium ruta-muraria*, *Camptosorus sibiricus*, *Thalictrum thunbergii*, *Clematis stans* var. *austrojaponensis*, *Angelica yoshinagae*, *Keiskea japonica*, *Anapharis sinica*, *Hosta tosana*, *Alectorurus yedoensis*, can be seen. On the other hand *Viola ovato-oblonga*, *Galium pogonanthum*, *Aster ageratoides* var. *semiamplexifolius*, *Liliope platyphylla*, *Cymbidium virescens*, etc. are commonly found as the companions.

As mentioned above, one of the characteristic features of this association is the dominance of *Carpinus turczaninovii*. But the communities found on Mt. Tsurugi and Mt. Ishidate are different from the typical stand by the absence of this species. Moreover, these communities are differentiated from the typical Carpinetum by the frequent occurrences of *Spiraea blumei*, *Potentilla fruticosa* var. *mandshurica*, *Aruncus syrvester*, *Gerenium shikokianum*, *Valeriana fauriei*, and others. (Table 5) At first, it was considered that these were united into an other association, but is now perceived that these stands represent a highland subassociation of this Carpinetum.

This subassociation, Zabelieto-Carpinetum spiraeetosum, is usually developed on cliffs or screes and is dominated by *Spiraea blumei* in the shrub layer and *Thalictrum thunbergii* in the herb layer respectively. This *Spiraea* is dominant in this community, but will be regarded as a characteristic species of the association on serpentine in Shikoku.

IV. Other Communities on Limestone Areas

As the result of the writer's investigations, the above-mentioned three associations are recognized as the edaphic or topographic climaxes developed on limestone outcrops in Shikoku. However, there are various stands on limestone areas, and some of them can be included in one of the above associations. For instance, open communities on cliffs and screes often contain the characteristic species of Zabelieto-Carpinetum.

On the contrary, even in limestone areas, the establishment of climatic climax forests can usually be seen on fertile and deep soils. The examples are found on Mt. Ishidate, Mt. Onogahara, etc., where Sasamorpheto-Fagetum[3], the deciduous broad-leaved climax forest, occurs. The same is the case with the evergreen broad-leaved forest on limestone areas in the vicinity of Kôchi city.

An other example, though not treated in this paper, is herbaceous communities often developed on moist and fertile soils. Such stands exist on Mt. Tsurugi, Mt. Ishidate, Mt. Torigata, etc. These herbaceous communities are dominated by

Table 3. Nandineto-

Locality	4	4	5	5	5	6	6	8	8
Altitude	200	200	280	280	285	100	100	50	50
Exposition	S85W	S75W	S40W	S60W	S30W	S40W	N70W	N60W	N60W
Steepness	20	20	5	10	5	20	30	30	20
2nd tree layer									
Cyclobalanopsis glauca	5(21)	5(21)	5(11)	5(2+)	5(2+)	4(1+)	5(21)	5(21)	3(32)
Tracherospermum asiaticum v. *intermedium*	1(12)	(12)	(−2)	(+3)	+(+2)	(+3)	+(24)	(+3)	(+3)
Ficus electa	1(2+)	2(1+)	1(1+)	1(2+)	2(1+)	(1+)	(+)	3(21)	(2+)
Xylosma japonicum	2(2)	−	(2)	1(2+)	1(1)	(++)	(1+)	(++)	−
Ligustrum japonicum	(1)	(1+)	−	(+)	(+)	−	(+)	1(21)	1(++)
Paederia scandens v. *mairei*	(−+)	(−+)	−	−	−	(−+)	(+1)	(+1)	(12)
Neolitsea sericea	−	(++)	(++)	−	(1+)	−	(+)	2(−+)	−
Elaeagnus pungens	(1+)	−	(+)	(+)	(+)	−	−	1(+)	1(++)
Euonymus alatus v. *rotundatus*	−	(+)	−	−	−	(1)	(+)	2	−
Pittosporum tobira	−	−	(2)	−	−	(1)	(+)	(−1)	(+)
Akebia trifoliata	−	−	−	−	(++)	(−1)	(−+)	−	(−1)
Helwingia japonica v. *parvifolia*	(2+)	(++)	(1)	−	−	−	−	−	−
Akebia quinata	−	−	2(−+)	1	−	−	(−+)	−	(21)
Clematis maximowicziana	−	(−+)	(−+)	−	−	−	−	−	−
Eriobotrya japonica	−	−	−	−	−	−	−	−	(+)
Arundinaria simonii	−	−	−	−	−	−	−	−	−
Melia azedarach v. *japonica*	−	−	−	−	−	−	−	−	−
Pinus densiflora	−	−	−	−	−	3	−	−	−
42 other species									
Shrub layer									
Nandina domestica	4(2)	3(2)	3(1)	2(+)	2(+)	+(+)	−	3(+)	2(+)
Kerria japonica	2(+)	1(+)	1(+)	2(+)	2(+)	3(2)	2(1)	−	−
Hedera rhombea	+(1)	+(1)	(2)	+(2)	+(1)	−	+(1)	(1)	(1)
Ficus foveolata	−	(+)	−	(1)	(1)	−	−	−	+(1)
Dioscorea gracillima	−	−	(+)	−	+(+)	(+)	(+)	+(+)	(+)
Lemmaphyllum microphyllum	(+)	(+)	−	−	−	(2)	−	(1)	(1)
19 other species									
Herb layer									
Ardisia japonica	+	+	−	1	1	+	2	−	−
Ophiopogon japonicus	1	1	+	1	2	1	−	2	2
Cymbidium virescens	1	+	2	+	+	−	−	+	+
Liliope platyphylla	2	3	2	3	2	−	1	3	3
Onychium japonicum	+	+	+	−	−	2	1	1	+
Clematis williamsii	1	−	+	+	−	1	+	+	+
Rubus buergeri	+	+	+	+	1	−	−	1	1
Oplismenus undulatifolius v. *japonicus*	−	−	+	−	+	1	−	2	2
Cyclosorus acuminatus	+	−	2	+	+	1	+	−	−
Carex sendaica v. *nakiri*	+	−	1	−	2	1	2	−	−
Carex makinoensis	−	−	−	−	−	−	−	−	2
Selaginella pachystachys	−	−	−	−	−	3	2	−	−
65 other species									

( ) = Dominance of the same species in the shrub and herb layers.

Comanthosphace, *Veronica*, *Ligularia*, *Cacalia*, *Circium*, etc. Though the structures of these communities are more or less different from one another, they present similar floristic compositions to the herbaceous communities on moister or alluvial soils in the *Fagus crenata* climax region.

Extensive limestone areas are often occupied by secondary communities chiefly caused

Cyclobalanopsidetum glaucae

9	9	12	13	13	17	17	20	22	24	24	Constancy	Fidelity
200	210	150	280	280	140	150	60	40	120	150		
S20W	S	S30E	S70W	S70W	S80E	S75W	S30W	E	S60W	S15E		
15	25	5	20	20	30	20	30	20	20	10		
5(11)	5(1+)	5(2+)	5(1+)	4(2+)	5(1)	5(21)	5(1+)	5(2+)	5(31)	5(2+)	V	3
(12)	(32)	(+2)	(+2)	(1+)	3(+2)	+(+2)	(+3)	(12)	(+3)	1(12)	V	2
(1)	(+2)	(+)	2(1+)	2(1+)	2(1+)	–	1(1)	2(+)	2(2+)	2(++)	V	2
1(2)	(1)	1(+)	2(++)	(++)	1(+)	1(+)	2	(++)	(+)	2(2+)	V	4
(11)	2(+)	1(21)	1(+)	–	–	2(++)	1(+)	2(1+)	1(2+)	3(2+)	IV	2
(–+)	–	–	–	–	(–+)	(–+)	(++)	(++)	+(++)	+(+1)	IV	2
(+)	(++)	–	–	1(+)	1(1+)	–	–	1(1+)	3(2+)	+(+)	III	2
(+)	–	–	–	(–+)	(+)	(++)	–	–	(+)	(1)	III	2
1(1)	(2)	–	(–+)	–	–	(+)	–	(++)	(+)	+	III	2
–	(1)	–	1(+)	1(+)	–	–	3(1)	–	–	+(+)	III	2
–	–	(–+)	+	–	(–+)	–	–	(–+)	(–+)	(++)	III	2
(++)	–	(+)	(1+)	–	+(++)	1(++)	–	(3+)	–	–	III	2
(–+)	(–+)	–	(–+)	–	–	(–+)	+(++)	–	–	–	III	2
(–+)	–	+(++)	(++)	(–+)	(+)	–	(–+)	–	–	(–+)	III	2
–	–	1(1)	2(2+)	2(+)	1(2+)	+(1)	–	(–+)	–	–	II	4
–	–	–	–	(1)	–	–	(3)	1(1+)	–	–	I	1
–	–	–	1	–	2	–	–	–	–	–	I	4
–	–	–	–	–	–	–	–	–	–	–	I	1
3(+)	2	2(1)	1(+)	–	3(+)	3(1)	–	4(1)	1	–	IV	5
–	–	–	1(+)	2	2(+)	3(+)	–	–	2(+)	3(1)	IV	2
(2)	(2)	(2)	(1)	–	–	–	+(3)	–	–	(2)	IV	2
1(1)	(1)	(+)	+(1)	+(1)	+(+)	–	–	+(+)	–	+(1)	II	2
–	–	(+)	(+)	–	(+)	–	–	+	(+)	(+)	III	2
(+)	(+)	–	–	–	–	+(1)	–	(1)	–	–	III	2
2	2	+	2	1	1	3	–	1	2	–	V	3
1	2	+	–	–	+	2	1	2	1	1	V	3
1	+	1	–	–	1	1	1	1	+	1	IV	2
3	2	2	2	1	2	2	–	–	–	–	IV	3
1	1	+	–	–	–	–	–	1	2	+	IV	3
1	–	1	–	–	1	+	–	–	+	+	IV	2
–	–	+	–	–	–	2	–	2	+	–	III	2
–	–	+	–	–	+	2	–	2	3	–	III	2
–	–	+	–	+	–	–	2	–	1	–	III	2
–	–	–	–	–	1	1	–	3	–	1	III	3
–	–	–	–	–	–	–	–	–	4	2	II	2
–	–	–	–	–	–	–	–	–	–	–	I	2

by human interferences. These areas are usually characterized by the dominant occurrences of *Arundinaria pygmaea*, *Sasa* spp., *Miscanthus sinensis*, etc. Sometimes, open pine forests dominated by *Pinus densiflora* are also found on these disturbed areas.

Table 4. Zabelieto-

Locality	2	3	9	9	10	10	13	13	13	13	17
Altitude	1250	950	220	220	285	280	400	400	380	360	155
Exposition	S	S55E	S20E	S30E	N80E	N80E	—	S55W	S30W	S30W	S50E
Steepness	30	35	30	40	35	35	0	25	15	30	10
2nd tree & Shrub layer											
Carpinus turczaninovii	3(+)	5(+)	5(1)	5(+)	5(+)	5(+)	4(+)	3(+)	4(+)	4(+)	3(4)
Euonymus alatus v. *rotundatus*	+	2	2	2	2(+)	1(+)	2(+)	3(+)	3(+)	3(+)	2(+)
Lespedeza buergeri	2(1)	1(+)	3(1)	3(1)	—	—	2(+)	1(+)	2(+)	3(+)	1(1)
Zabelia integrifolia	2(+)	2(+)	1(+)	—	—	—	3(1)	3(+)	(+)	—	2(+)
Paederia scandens v. *mairei*	—	—	(+)	+(+)	+(+)	+(+)	+(+)	(+)	+(+)	(+)	(1)
Rosa lusiae v. *onoei*	+(+)	1(+)	+	(+)	1(+)	+(+)	(+)	+(+)	2(+)	1(+)	+(+)
Fraxinus sieboldiana v. *serrata*	1(+)	—	—	—	—	—	+(+)	1(+)	—	—	+
Spiraea nervosa	—	—	—	—	—	—	1	3(+)	—	1(+)	3(+)
Cyclobalanopsis glauca	—	—	3(+)	2(+)	1(+)	+(+)	—	1(+)	2(+)	+(+)	2(+)
Tracherospermum asiaticum v. *intermedium*	—	—	(2)	+(2)	+(3)	(3)	(2)	+(+)	(+)	(2)	(+)
Torreya nucifera	—	3(+)	—	—	2(+)	3(+)	—	—	—	—	—
Smilax sieboldi	—	+(+)	—	—	—	—	—	(+)	—	+(+)	(+)
Dioscorea gracillima	—	—	(+)	(+)	+(+)	+(1)	(+)	(+)	(+)	(+)	(+)
Kerria japonica	—	3(+)	—	—	—	—	(+)	+(+)	3(1)	2(1)	—
Ligustrum japonicum	—	—	2	2	+	2	2	+(+)	3(+)	2(+)	+(+)
Picrasma quassioides	—	—	1	2	—	1	—	+	—	2	—
Pitosporum tobira	—	—	—	1	3(+)	+	(+)	3	—	—	+
Buxus microphylla v. *japonica*	—	—	—	—	—	—	1(2)	+(1)	1(+)	—	1(+)
Smilax stans	—	—	—	—	—	—	—	—	—	—	—
Rhamnus yoshinoi	—	—	—	—	—	—	—	+(+)	—	—	3(+)
Abelia spathulata	—	—	+(+)	—	—	—	—	—	—	—	1
Lindera obtusiloba	2(+)	3	—	—	—	—	—	—	—	—	—
Pertya glabrescens	—	+(+)	—	—	—	—	—	—	—	—	—
Pinus densiflora	—	—	—	—	—	—	4	—	—	—	—
Quercus serrata	—	—	—	—	—	—	3(+)	—	—	—	—
Dioscorea tenuipes	—	—	—	—	—	—	—	—	—	—	—
Securinega suffruticosa	—	—	—	—	—	—	—	—	—	3(+)	—
Rhamnus japonica v. *decipiens*	(+)	—	—	—	—	—	—	—	—	—	—
Arundinaria pygmaea v. *glabra*	—	—	—	—	—	—	5(+)	—	—	—	—
Sabina chinensis	3	—	—	—	—	—	—	—	—	—	—
Tsuga sieboldii	3	—	—	—	—	—	—	—	—	—	—
Chamaecyparis obtusa	—	—	—	—	—	—	—	—	—	—	—
Vitis yokogurana	—	—	—	—	—	—	—	—	—	—	—
93 other species											
Herb layer											
Miscanthus sinensis	—	—	+	+	1	—	+	1	+	+	1
Cymbidium virescens	—	+	2	2	—	+	+	+	—	1	+
Galium pogonanthum	—	—	+	—	—	+	+	1	1	—	+
Clematis williamsii	—	—	+	+	+	+	1	+	+	—	1
Viola ovato-oblonga	—	—	—	+	+	—	+	+	1	+	1
Ophiopogon japonicus	—	+	2	2	1	1	—	2	+	1	+
Oplismenus undulatifolius v. *japonicus*	—	—	—	+	2	1	+	—	+	1	+
Ardisia japonica	—	—	1	—	2	2	2	+	1	—	—
Aster ageratoides v. *semiamplexifolius*	—	—	—	+	+	—	—	—	—	—	—
Carex makinoensis	—	—	—	—	—	—	—	—	—	—	2
Thalictrum thunbergii	—	—	—	—	—	—	+	+	+	—	2
Hosta tosana	—	—	3	3	5	+	—	—	—	—	2
Camptosorus sibiricus	—	+	—	—	—	+	—	—	—	—	—
Keiskea japonica	—	—	—	—	—	—	—	—	—	—	—
Alectorurus yedoensis	—	—	—	—	—	—	—	—	—	—	2
Selaginella pachystachys	—	—	—	—	2	4	—	—	—	—	2
Carex fernaldiana	—	—	—	—	—	—	—	—	—	—	—
Angelica yoshinagae	—	—	—	—	—	—	—	—	—	—	1
Carex duvaliana	2	—	—	—	—	—	—	—	—	—	—

Carpinetum turczaninovii

17	17	25	25	25	25	27	28	28	29	29	29	31	31	Constancy	Fidelity
155	150	820	810	810	810	1450	860	850	510	520	510	380	400		
S35W	S55W	N65W	S40E	S15E	S20E	S25E	S35E	NSEW	S40E	S40E	N80E	S15W	N70E		
30	20	20–80	25	50	50	10	35	0–30	30	45	35	35	20		
3(+)	4(+)	3(1)	5(+)	4(+)	4(1)	4(+)	2(+)	4(+)	2(+)	3(+)	5(+)	4(+)	4(+)	V	5
3(+)	1(+)	1(+)	1(+)	+(+)	1(+)	+	+	2(+)	2(+)	2	+	1(+)	1	V	3
1(+)	2(1)	2(+)	1(+)	1	2(1)	—	2(1)	2(1)	3(2)	3(+)	2(+)	2(2)	(+)	V	2
2(+)	1	2(1)	(+)	—	3(1)	3(+)	2(1)	2(+)	4(1)	2(+)	3(2)	2	3(2)	IV	5
+(+)	(+)	—	(1)	(+)	(2)	—	—	+(+)	(+)	(1)	(+)	—	(+)	IV	2
2(+)	+(+)	—	—	—	—	1	—	2(+)	(+)	—	—	—	—	IV	3
3(+)	3	1(+)	—	1	+	2(+)	2	2(+)	—	1(+)	—	+	1	III	2
2(+)	+	2(1)	(+)	2(1)	1(+)	2(+)	—	—	—	—	—	3(1)	—	III	5
2(+)	+	—	—	—	—	—	—	—	—	—	—	2(+)	2(+)	III	2
(1)	(1)	—	—	—	—	—	—	—	—	(2)	—	—	—	III	2
—	—	(+)	2(+)	1	—	—	—	—	2(+)	1(+)	2(+)	(+)	(+)	III	4
1(1)	+(+)	—	—	—	—	—	—	—	(+)	(+)	+	(+)	1	III	2
+(+)	+(+)	—	—	—	—	—	—	—	—	—	—	—	—	III	2
2(2)	3(2)	—	—	—	—	—	—	—	2(+)	3(+)	4(2)	—	—	II	2
—	+	—	—	—	—	—	—	—	—	—	—	—	—	II	2
1	3	—	—	—	—	—	—	—	—	—	1	—	—	II	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	II	2
2(+)	+	—	—	—	—	—	—	—	—	—	—	—	—	II	3
—	—	—	—	—	—	—	+(+)	+	1(+)	1(1)	+(+)	—	—	I	5
3(+)	+	—	—	—	—	—	—	—	—	—	—	—	—	I	5
—	2(+)	—	—	—	—	—	—	—	—	—	—	—	3(+)	I	3
—	—	—	—	—	—	—	(+)	—	—	—	—	+	—	I	2
—	—	—	—	—	—	—	—	—	3(1)	+(+)	2(+)	—	—	I	2
—	—	—	—	—	—	—	3(+)	—	—	—	—	—	+	I	1
—	—	—	—	—	—	—	1(+)	—	—	—	—	—	1	I	2
—	—	—	—	—	—	—	(+)	(+)	—	—	+(+)	—	—	I	3
+	—	—	—	—	—	—	—	—	—	—	—	—	—	I	2
—	—	—	—	—	—	+	—	—	—	—	—	—	—	I	3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	1
—	—	—	—	—	—	—	3(+)	—	—	—	—	—	—	I	1
—	—	—	—	—	+	—	—	—	—	—	—	—	—	I	5
+	1	—	—	+	1	+	2	1	1	1	1	+	+	IV	2
+	1	—	—	—	—	—	—	+	+	+	+	2	1	IV	2
+	+	+	1	+	—	—	—	—	+	+	+	+	+	IV	2
2	—	—	+	—	—	—	—	—	1	1	+	—	—	III	2
+	+	+	—	—	+	—	—	—	+	+	—	—	—	III	2
—	1	—	—	—	—	—	—	—	+	+	—	—	—	III	2
+	+	—	—	—	—	—	—	—	+	+	+	—	—	III	2
+	—	—	—	—	—	—	—	—	+	+	+	—	+	III	2
—	—	+	+	1	1	1	—	—	—	+	+	—	+	III	2
5	1	2	3	3	3	—	—	—	—	—	2	3	2	II	3
3	2	—	—	+	+	3	—	+	—	—	—	—	—	II	3
2	2	—	—	—	—	—	—	—	—	—	—	—	—	II	4
—	—	—	—	—	—	—	—	—	+	+	+	+	+	II	3
1	—	—	2	1	2	—	—	—	—	—	—	—	—	I	3
2	+	—	—	+	—	—	—	—	—	—	—	—	—	I	3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	2
—	—	2	1	—	+	—	—	—	3	2	—	—	—	I	2
+	1	—	—	—	—	—	—	—	—	—	—	—	—	I	4
—	—	—	—	—	—	1	—	—	—	—	—	—	—	I	2

Locality	2	3	9	9	10	10	13	13	13	13	17
Altitude	1250	950	220	220	285	280	400	400	380	360	155
Exposition	S	S55E	S20E	S30E	N80E	N80E	—	S55W	S30W	S30W	S50E
Steepness	30	35	30	40	35	35	0	25	15	30	10
Carex ciliatomarginata	3	—	—	—	—	—	—	—	—	—	—
Anaphalis sinica	+	—	—	—	—	—	—	—	—	—	—
Carex humilis v. *nana*	—	—	—	—	—	—	—	—	—	—	—
Carex conica?	—	—	—	—	—	—	—	—	—	—	—
Carex autamnalis	—	2	—	—	—	—	—	—	—	—	—
Clematis stans v. *austrojaponensis*	—	—	—	—	—	—	—	—	—	—	—
Amesium ruta-muraria	—	—	—	—	—	—	—	—	—	—	—
Buckleya lanceolata	—	+	—	—	—	—	—	—	—	—	—
86 other species											

( ) = Dominance of the same species in the herb layer.

V. Physiognomic and Floristic Characters of the Limestone Vegetation

Though physiognomic and structural characters of the three associations recognized in this survey are fairly different from one another, they have some common characteristics or tendencies which are different from the adjacent vegetation on other rocks.

Closed and well-developed communities occur on limestone where the ground is stable enough to allow the existence of a humus layer. However, because of the dry character of most limestone outcrops, the vegetation under such circumstances is usually stunted and dwarf shrub communities which are dominated by deciduous micro- or nanophanerophytes having microphylls. This physiognomic character is very conspicuous in Zabelieto-Carpinetum developed on dry and rocky ridges. In spite of the dominance of evergreens in Nandineto-Cyclobalanopsidetum, deciduous shrubs having microphylls are relatively abundant in species, too. On the other hand, in Orixetum japonicae occurring on moister sites, dominant microphanerophytes are usually deciduous and have mesophylls.

The floristic composition of limestone vegetation is also characteristic, containing a large number of so-called calcicolous plants. The limestone flora: (1) is often dominated by certain families or genera, (2) contains relic and endemic species, (3) includes some shore and a pine plants on areas far away from sea and high mountains. Therefore the limestone flora is very complex. It is often recognized that northern or southern plants respectively have their southern or northern outposts on limestone areas. These interesting problems on the flora on limestone were already reported[4),5),6),8)] or will be published later by the writer.

Some species occurring on limestone are the association characteristics, while other plants are not specially connected with any particular associations. From the floristic compositions and physiognomic features of limestne vegetation, it may be impossible to include different associations in one and the same alliance.

Finally, it may be stated that the study on the chemical and physical properties of rock and soil of limestone affecting the vegetation is perhaps one of the most important problems. However, this is not treated in this paper, since the main object of this paper is an analytical study of the vegetation.

														Constancy	Fidelity
17	17	25	25	25	25	27	28	28	29	29	29	31	31		
155	150	820	810	810	810	1450	860	850	510	520	510	380	400		
S35W	S55W	N65W	S40E	S15E	S20E	S25E	S35E	NSEW	S40E	S40E	N80E	S15W	N70E		
30	20	20–80	25	50	50	10	35	0–30	30	45	35	35	20		
—	—	—	—	—	—	4	—	—	—	—	—	—	—	I	2
—	—	—	—	2	—	—	—	—	—	—	—	—	—	I	5
—	—	—	—	—	—	—	3	2	—	—	—	—	—	I	4
—	—	—	—	—	—	—	—	—	—	—	—	—	3	I	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	4
—	—	—	—	—	—	1	—	—	—	—	—	—	—	I	5
—	—	—	—	+	—	—	—	—	—	—	—	—	—	I	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	I	3

Table 5. Zabelieto-Carpinetum spiraeetosum

Locality	1	1	2	2		2	1	2	2
Altitude	1759	1800	1600	1590		1750	1800	1600	1590
Exposition	N70W	S	S65W	N10E		N70W	S	S65W	N10E
Steepness	25–80	80–90	30	35		25–80	80–90	30	35
Shrub layer					Herb layer				
Spiraea blumei	4	4	—	3	*Thalictrum thunbergii*	4	2	2	3
Rhamnus japonica v. *decipiens*	+	—	3	2	*Valeriana fauriei*	1	1	2	2
Salix sp.	—	—	2	3	*Geranium shikokianum*	1	1	2	1
Zabelia integrifolia	—	—	2	2	*Aruncus syrvester*	+	1	2	2
Abelia spathulata	1	—	—	2	*Ligularia stenocephala* v. *oligantha*	+	1	+	—
Deutzia gracilis	2	+	—	—	*Bistorta major* v. *nitens*	—	+	+	+
Fraxinus sieboldiana v. *serrata*	1	—	+	—	*Veratrum maackii*	—	—	2	1
Abies homolepis	1	—	—	+	*Adenophora remotiflora*	—	—	1	1
Tilia japonica	+	—	—	—	*Arabis gemmifera*	1	+	—	—
Spiraea japonica	—	—	+	—	*Festuca ovina* v. *chiisanensis*	1	+	—	—
Potentilla fruticosa v. *mandshurica*	—	—	(+)	+	*Anaphalis sinica*	—	—	+	+
Tsuga diversifolia	2	—	4	—	*Saussurea amabilis*	—	—	+	+
Carpinus carpinoides	—	—	—	—	*Galium kinuta*	—	—	—	3
Pertya glabrescens	—	—	—	2	*Filipendula tsugiwoi*	—	—	2	—
Hydrangea macrophylla v. *acuminata*	—	—	—	2	*Galium kamtschaticum* v. *acutifolium*	—	—	2	—
9 other species	—	—	2	—	*Carex blepharicarpa*	—	2	—	—
					13 other species				

VI. Summary

1. The Vegetation on limestone outcrops in Shikoku was studied from a standpoint of phytosociology.

2. Three distinct associations were recognized and described in detail.

3. Orixetum japonicae is a deciduous shrub community developed on shady and moist sites. Nandineto-Cyclobalanopsidetum glaucae is a stunted evergreen oak forest, usually found on mountainsides in the warm-temperate forest region. Zabelieto-Carpinetum turczaninovii occupies dry and unstable ridges or mountainsides, and is a community mainly composed of deciduous shrubs.

4. Physiognomic characters and floristic compositions of these associations con-

trast strikingly with those of the adjacent vegetation on other soils.

5. There are many stands which cannot be included in any of the above associations on limestone areas. They are scarcely treated in this paper. The problems on the relations between the flora and limestone soils will be discussed in the near future.

VII. Literature cited

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(Received June 30, 1955)