PROGRESSIVE AND RETROGRESSIVE GRADIENT OF GRASSLAND VEGETATION MEASURED BY DEGREE OF SUCCESSION—ECOLOGICAL JUDGEMENT OF GRASSLAND CONDITION AND TREND IV[1])

by

MAKOTO NUMATA

Department of Biology, Chiba University, Japan

INTRODUCTION

The grassland vegetation in Japan, as formerly stated by the author (NUMATA 1961), is not the climatic climax but seral stages of plant succession controlled by edaphic or biotic conditions, except alpine grasslands in the highest life zone over the tree line of mountains. Especially grasslands under cultural or anthropoic suppressions used for grazing and mowing, or burnt are almost mesic seral stages. The grassland vegetation under natural suppressions as avalanche, strong wind, etc. is also a seral stage of secondary succession.

After the Second World War, the Ministry of Agriculture and Forestry has tried to estimate the carrying capacity of cattle in the semi-natural or artificial grasslands in Japan. The productivity of such grasslands as the field of secondary production of domestic animals must be estimated by some quantitative measures. The orientation of various kinds of grassland in the course of secondary succession must be given from the ecological standpoint and, in addition, the relationship of the productivity of a grassland to its seral status must be elucidated.

The author and his collaborators have analysed phytosociologically pioneer and following grassy stages of secondary succession, as related to floristic composition and life-form spectrum (NUMATA & YAMAI 1955, NUMATA 1956, NUMATA & SUZUKI 1958), dispersive structure, especially the type and mode of distribution of plants (NUMATA 1954, 1961, 1966), progressive succession from herbaceous stage to arborescent stage (OHGA & NUMATA 1965), relations between buried-seed population in the soil and actual above-ground vegetation (NUMATA et al. 1964, NUMATA, AOKI & HAYASHI 1964, HAYASHI

---

1) Contribution from JIBP-CT No. 14. This is partly supported by the special project research "Studies on the dynamic status of biosphere" sponsored by the Ministry of Education.

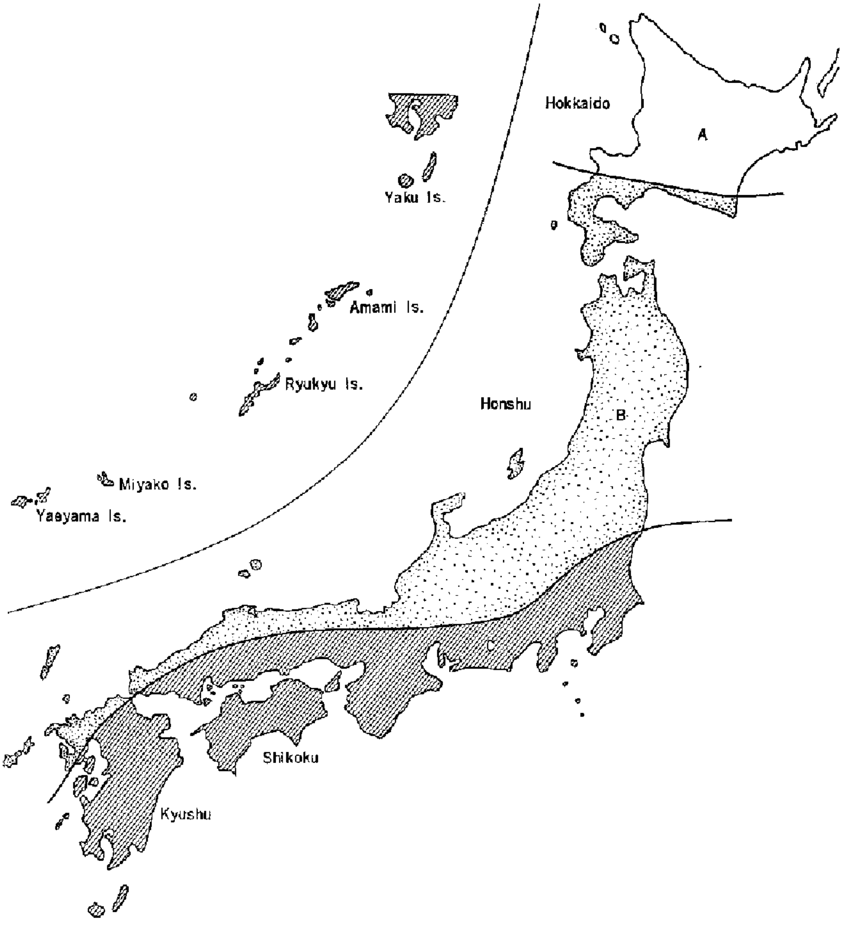

Fig. 1. The horizontal zones of grassland vegetation in Japan. When m and p show grasslands under mowing (meadows) and grazing (pastures) respectively, there are zones of Am: *Sasa* type, Ap: *Poa pratensis* type, Bm: *Miscanthus sinensis* type, Bp: *Zoysia japonica* type, Cp: *Miscanthus-Pleioblastus* type, and Cm: *Pleioblastus distichus* var. *nezasa* type. The border between A and B coincides with the northern limit of the *Fagus crenata* climax zone. The climates of A, B, and C are subarctic or cold temperate, cool temperate and Japan-Sea side type, and warm temperate respectively.

& NUMATA 1964, 1966, 1967), ecological judgement of grassland condition and trend (NUMATA 1965, 1966, 1966), etc.

In connection with experimental works mentioned above, the author has surveyed grasslands used for grazing and mowing all over the country from north to south. As the results of this survey

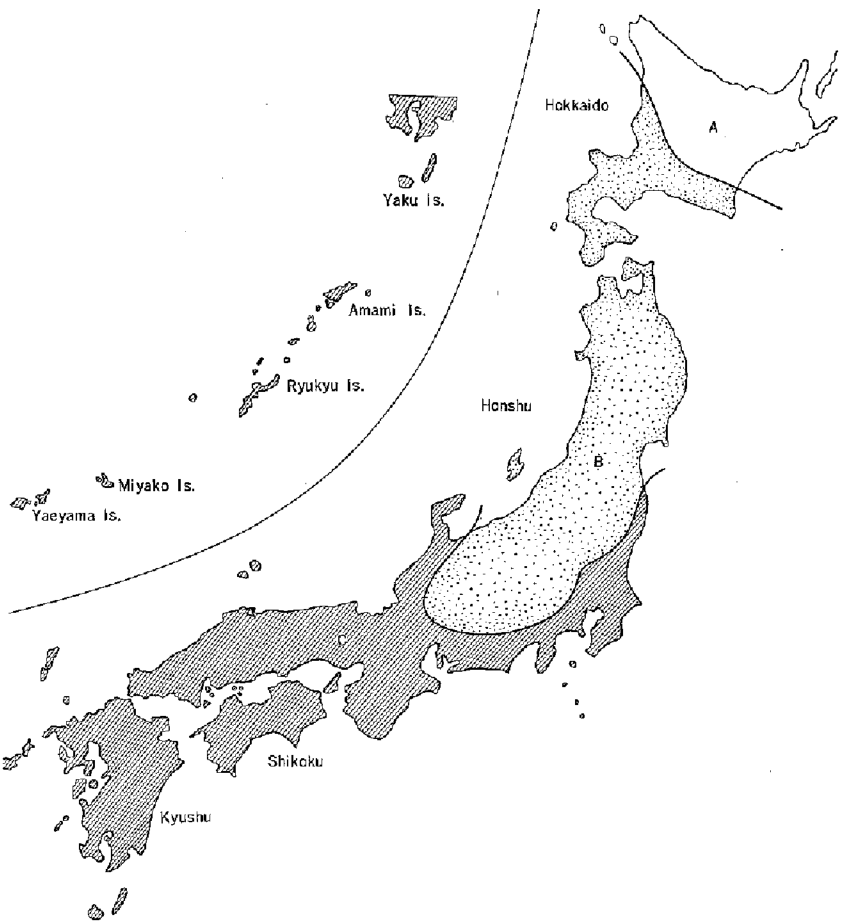

Fig. 2. The horizontal zones of climax forests of Japan drawn by the author referring to HONDA (1900), MIYAWAKI & ITOW (1966) and SUZUKI (1966). A: evergreen needle-leaved formation, B: deciduous broad-leaved formation, C: evergreen broad-leaved formation.

since 1957, 1) different courses of plant succession corresponding to each climatic type, and 2) vegetation types of grassland used for grazing and mowing corresponding to each climatic type are elucidated. However the grassland vegetation zones (Fig. 1) deviate from the climax forest zones (Fig. 2) and the pine forest zones as one of the secondary forest zones (Fig. 3).

In this paper the author wishes to describe the outline of his survey and to discuss the progression and retrogression of plant succession measured quantitatively by the degree of succession.

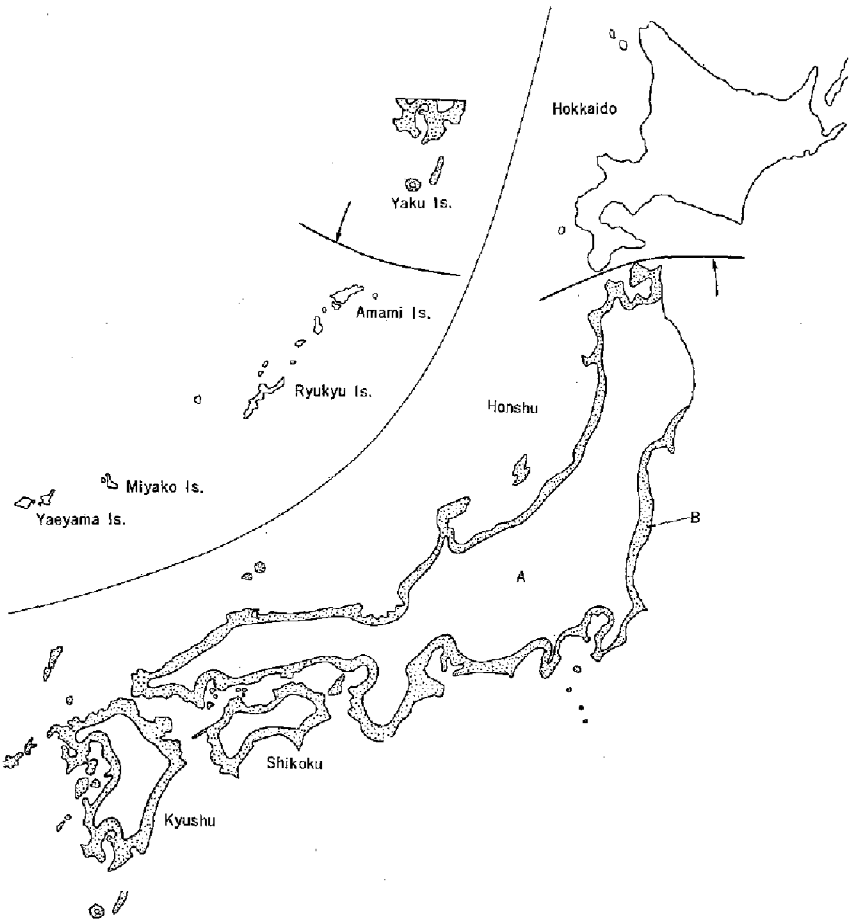

Fig. 3. The pine forest zones of Japan drawn by the author referring to YOSHIÔKA (1958) and CRITCHFIELD & LITTLE (1966). A: *Pinus densiflora* inland forest, B: *Pinus Thunbergii* coastal forest.

LOCAL MODIFICATION OF THE COURSE OF PLANT SUCCESSION

Formerly OSEKO (1937) studied and formulated the course of succession in grasslands as the main course of waste stage — *Zoysia* stage — *Miscanthus* stage — forest stage with branches of *Sasa-*, *Lespedeza-*, cryptogam(fern)-, brushwood-, and coppice, pinewood stages. YOSHIDA (1950, 1956) and SHIMADA (1961) also recognized the similar course of seral stages.

However this scheme is limited to the north-eastern Japan in the cool-temperate region (NUMATA 1961). As grazing lands, the

Zoysia stage is of the cool-temperate region, and the *Pleioblastus* stage and the *Poa pratensis* stage appear in the warm-temperate and cold-temperate or subarctic regions respectively instead of the *Zoysia* stage. That is, the species of *Zoysia japonica* is distributed widely from southern Hokkaido to Kyushu, however it dominates only at the cool-temperate pastures in the *Fagus crenata* zone (the Tohoku district and corresponding altitudinal zones). Pastures having a physiognomy like the *Zoysia*-type pasture are dominated by *Pleioblastus* (dwarf bamboo) in the southern half of Japan where the growth form of *Pleioblastus* is very similar to *Zoysia*. The natural growth of *Pleioblastus* shows heights of 2—3 m but the growth under grazing shows heights of 10 cm or so very likely to a short grass as *Zoysia*. Recently ITOW (1968, unpublished) has pointed out that there are grasslands of *Miscanthus*-type and *Zoysia*-type lacking *Pleioblastus disticus* var. *nezasa* in north-western Kyushu. Grasslands of *Pleioblastus*-type and *Pteridium*-type in Kyushu are distributed in the central part more than 700 m in altitude and more than 20 km apart from the coast, and grasslands lacking *Pleioblastus* are found in the coastal area (less than 5 km from the coast) less than 300 m in altitude.

Miscanthus sinensis is distributed more widely than *Zoysia japonica* in meadows (grasslands used for mowing) of Japan from north to south, however a wide-range homogeneous meadow is difficult to be established in north-eastern Hokkaido, because the tempo of the progression of secondary succession is slow and the competing power of *Miscanthus sinensis* against *Sasa* is relatively weak. In the subarctic region of north-eastern Hokkaido, *Sasa* is more predominant than *Miscanthus sinensis*. The types of grassland vegetation and their successional relationships correspond to the difference of the climatic region (Table I). Biotic and edaphic conditions affect the grassland vegetation within the frame of climatic conditions. The rate of decomposition of organic matters of soil is different according to grassland types. Therefore, the high-grass type meadow dominated by *Miscanthus sinensis*, etc. has deeper humus layer, richer moisture content, and higher contents of humus, total nitrogen, available nitrogen and exchangeable bases than in the short-grass type pasture dominated by *Zoysia japonica* (Agricultural Research Council of Ministry of Agriculture and Forestry 1959).

Dwarf-bamboo type grasslands (pastures and meadows) have often lower contents of humus, nitrogen, phosphoric acid, and calcium than high-grass type meadows dominated by *Miscanthus sinensis*. Grazing land is usually trampled to make compact soils, covered by the *Zoysia* type vegetation, and has often a thin surface-soil according to the erosion. Therefore the grazing land has, in general, lesser contents of calcium and magnesium, humus, ex-

TABLE I

Relationships between climatic regions and courses of secondary succession in Japan. On the latter, the plagiosere in the grassland succession is divided from the orthosere in the abandoned field. I: deteriorated or 1st (year) pioneer stage, II: shortgrass type grazing land or 2nd (year) pioneer stage, III: highgrass type mowing land or perennial grass stage, IV: shrubby stage, V: pioneer tree stage, VI: climax stage. Each stage is expressed by dominant or commonest species.

Stage	Subarctic region	
	Plagiosere	Orthosere
I	*Poa annua* L. *Cerastium caespitosum* GILIB. var. *ianthes* HARA *Polygonum Persicaria* L. *Rumex Acetosella* L.	*Digitaria violascens* LINK. *Polygonum Persicaria* L. *P. perfoliatum* L.
II	*Poa pratensis* L. *Phleum pratense* L. *Trifolium repens* L. *Hydrocotyle ramiflora* MAXIM. *Artemisia margaritacea* BENTH. & Hooker f.	*Erigeron* spp. *Agrostis palustris* HUDSON *Artemisia montana* PAMP. *Rudbeckia laciniata* L. *Epilobium angustifolium* L.
III	*Sasa nipponica* MAKINO & SHIB. *Miscanthus sinensis* ANDERS. *Pteridium aquilinum* KUHN	*Sasa nipponica* MAKINO & SHIB. *S. veitchii* REHD. *S. kurilensis* MAKINO & SHIB. *Miscanthus sinensis* ANDERS. *Calamagrostis Langsdorffi* THRIN. *Thalictrum Thunbergii* DC.
IV	*Lespedeza bicolor* TURCZ. *Rosa rugosa* THUNB. *Hydrangea paniculata* SIEB. *Cerastrus orbiculatus* THUNB. var. *strigillosus* MAKINO *Rubus phoenicolasius* MAXIM.	*Sorbus commixta* HEDL. *Vaccinium Smallii* A. GRAY *Sambucus Sieboldiana* BL. var. *Miquelli* HARA *Aralia elata* SEEM. *Rhus orientalis* SCHNEID.
V	*Betula platyophylla* SUKAT. var. *japonica* HARA *Alnus tinctoria* SARG. var. *velutina* HARA *Quercus mongolica* FISCH.	
VI	*Abies sachalinensis* FR. SCHM. *Picea jezoensis* CARR. *Taxus cuspidata* SIEB. & ZUCC.	

Stage	Cool-temperate region	
	Plagiosere	Orthosere
I	*Poa annua* L. *Digitaria violascens* L. *Rumex obtusifolius* L. *Carex nubigera* D. DON subsp. *albata* T. KOYAMA *Agrimonia Eupatria* L. var. *pilosa* MAKINO	*Digitaria adscendens* HENR. *D. violascens* L. *Polygonum Persicaria* L. *P. nodosum* L.

II	*Zoysia japonica* STEUD. *Carex nervata* FR. & SAV. *Ranunculus japonicus* THUNB. *Hydrocotyle ramiflora* MAXIM. *Luzula campestris* DC. var. *capitata* MIQ. *Geranium Thunbergii* SIEB. & ZUCC.	*Erigeron annuus* PERS. *E. canadensis* L. *Agrostis palustris* HUDSON *Artemisia vulgaris* L. var. *indica* MAXIM.
III	*Viola obtusa* MAKINO *Miscanthus sinensis* ANDERS. *Pteridium aquilinum* KUHN *Sasaella ramosa* MAKINO	*Miscanthus sinensis* ANDERS. *Arundinella hirta* TANAKA *Spodiopogon sibiricus* TRIN. *Pteridium aquilinum* KUHN
IV	*Lespedeza bicolor* TURCZ. var. *japonica* NAKAI *Salix bakko* KIMURA *Weigela hortensis* C. A. MEY *Rhododendron japonicum* SURING. *Salix vulpina* ANDERS.	*Stephanandra incisa* ZABEL *Symplocos chinensis* DRUCE var. *leucocarpa* OHWI *Viburnum dilatatum* THUNB. *Rhus javanica* L. *Corylus Sieboldiana* BLUME
V	*Betula platyphylla* SUKAT. var. *japonica* HARA *Pinus densiflora* SIEB. & ZUCC. *Pinus Thunbergii* PARL.	
VI	*Fagus crenata* BLUME *Acer Miyabei* MAXIM. *Quercus crispula* BLUME	

Stage	Warm-temperate region	
	Plagiosere	Orthosere
I	*Poa annua* L. *Digitaria adscendens* HENR. *Microstegium vimineum* A. CAMUS *Plantago asiatica* L.	*Ambrosia artemisiifolia* L. *Digitaria adscendens* HENR. *Polygonum Blumei* MEISN. *Setaria viridis* BEAUV.
II	*Pleioblastus distichus* MUROI & H. OKAM. var. *nezasa* MUROI *Zoysia japonica* STEUD. *Artemisia vulgaris* L. var. *indica* MAXIM. *Hydrocotyle maritima* HONDA	*Erigeron annuus* PERS. *E. canadensis* L. *E. sumatrensis* RETZ. *Oenothera parviflora* L. *Bromus unioloides* H. B. & KUNTH *Chenopodium album* L. *Artemisia vulgaris* L. var. *indica* MAXIM.
III	*Pleioblastus distichus* MUROI & H. OKAM. var. *nezasa* MUROI *Miscanthus sinensis* ANDERS. *Pteridium aquilinum* KUHN	*Imperata cylindrica* BEAUV. var. *Koenigii* DUR. & SCH. *Miscanthus sinensis* ANDERS. *Pleioblastus Chino* MAKINO *P. distichus* MUROI & H. OKAM. var. *nezasa* MUROI *Gleichenia dichotoma* HOOK.
IV	*Lespedeza bicolor* TURCZ. var. *japonica* NAKAI *L. cyrtobotrya* MIQ.	*Viburnum erosum* THUNB. *Rhododendron dilatatum* MIQ. *Rh. Kampferi* PLANCH.

	Rosa multiflora THUNB.	*Deutzia crenata* SIEB. & ZUCC.
	Lyonia Neziki NAKAI & HARA	*Clethra barbanervis* SIEB. & ZUCC.
	Pieris japonica D. DON	
	Smilax China L.	
	Wikstroemia Gampi MAXIM.	
V	*Pinus densiflora* SIEB. & ZUCC.	
	P. Thunbergii PARL.	
	Quercus serrata THUNB.	
	Q. dentata THUNB.	
VI	*Machilus Thunbergii* SIEB. & ZUCC.	
	Shiia Sieboldii MAKINO	
	S. cuspidata MAKINO	
	Lithocarpus edulis NAKAI	
	evergreen *Quercus* (*Q. acuta* THUNB., *Q. gilva* BLUME, etc.)	

changeable capacity, degree of saturation, etc. But it has great contents of total nitrogen, available nitrogen, particularly NO_3-N and available phosphoric acid. These influences are greater in the shallower soil layer. However, the action and reaction between grassland vegetation and edaphic-biotic factors in the course of the progression of secondary succession must be examined to the minutest details (NUMATA 1961).

In case of sown pasture, the pioneer stage is a mixed stand of orchard grass, red clover, Italian ryegrass, etc. In all Japan except Hokkaido, such a sown pasture is invaded by many weeds and becomes a deteriorated semi-natural grassland following natural succession. Orchard grass, red clover, etc. as northern type forage plants decline their growth in a pasture according to the high temperature and drought in summer (KAWANABE 1956, 1957).

Decline of legumes compared with grasses in the early stage of the establishment of a sown pasture is well known in Japan. It is not only based on the compensative role of legumes to grasses (McCLOUD & MOTT 1953), but on several causes of shortage of phosphate in the volcanic ash soil widely distributed in Japan, shortening of life span of northern type forage plants under the warm climate, etc. We have another contrary case where grasses decline their growth instead of legumes. It is caused by a high moisture content of soil, small absorption power of phosphoric acid in soils except the volcanic ash soil, insect damage (for example, *Prodenia litura* FABRICIUS grazing legumes), etc. These various factors modifying the course of secondary succession must be studied in different areas.

JUDGEMENT OF CONDITION OR ECOLOGICAL GRADIENT IN GRASSLANDS BY DEGREE OF SUCCESSION

As mentioned above, the distribution of vegetation types of grassland is *Poa pratensis* type — *Zoysia japonica* type — *Pleioblastus*

Table II

Characteristics of *Miscanthus sinensis* type grasslands

Number	6126-a	6128-c	6224	6254	6255	6257	6277	6279	6314	6315	6321	6326	6337
Location	Chugoku Agr. Expt. Sta., Ota-shi Shimane Pref.	Tatsumi, Konda-machi Hyogo Pref.	Horobetsu, Shari-machi Hokkaido	Asama Pasture Gumma Pref.	"	"	Mt. Oishi Wakayama Pref.	Chugoku Mountain Range, Hyogo Pref.	Kamisarabetsu Hokkaido	"	Rokkaku Kawatabi Farm Miyagi Pref.	"	Odai-yama Tomiyama, Chiba Pref.
Use	Mowing	No use	No use	Weak grazing	"	"	No use	Mowing	"	After cultivation	Burning, no use	After cultivation	Mowing
Dominant	*Miscanthus sinensis*	"	"	"	"	"	*Miscanthus sinensis*	"	"	"	"	"	"
v	1.0	1.0	1.0	0.7	1.0	0.5	1.0	1.0	0.8	0.5	1.0	1.0	1.0
n	23	36	11	28	35	63	11	31	22	18	19	17	45
DS	326	451	995	255	449	175	329	554	414	281	415	183	316
SDR	100	100	94.2	82.0	100	100	100	100	83.3	100	96.6	100	92.7
SDR′	19.7	27.0	24.6	21.6	14.9	11.3	32.0	10.8	11.8	14.6	19.1	47.2	9.7

6261	6264	6266	6270	6271	6272	6273	6276
Mineoka-machi Chiba Pref.	Sangao, Noda-shi Chiba Pref.	Anagawa, Chiba-shi Chiba Pref.	Sata-machi Kagoshima Pref.	Mt. Oishi Wakayama Pref.	,,	,,	,,
No use	,,	,,	,,	Mowing	,,	,,	,,
,,	,,	,,	,,	,,	,,	,,	,,
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
61	32	17	19	42	42	36	24
544	710	416	789	266	350	326	179
100	94.8	92.1	100	100	92.3	100	100
7.1	16.0	26.3	14.9	9.7	9.9	12.0	22.6

6353-a	6353-b	6401	6426	6427	6428	6438	6611
Expt. Plot Kawatabi, Miyagi Pref. 10 June	,, 14 Sept.	Hokizawa Mt. Tanzawa Kanagawa Pref.	Yabitsu, Mt. Tanzawa Kanagawa Pref.	,,	1000 m alt. Mt Tanzawa Kanagawa Pref.	Mt. Omuro Kanagawa Pref.	IBP Area Kawatabi Miyagi Pref.
No use	,,	,,	,,	,,	,,	,,	,,
,,	,,	,,	,,	,,	,,	,,	,,
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
23	27	30	23	23	21	22	28
295	222	774	643	424	607	593	343
89.4	100	75.0	89.2	83.5	100	78.0	100
18.5	21.9	5.3	14.5	14.2	20.5	17.2	17.3

disticus var. *nezasa* type in case of grazing land and *Sasa nipponica* or *Sasa veitchii* type — *Miscanthus sinensis* type — *Miscanthus sinensis-Pleioblastus disticus* var. *nezasa* type in case of mowing land from north to south corresponding to the climatic regions (NUMATA 1961, SUGANUMA 1966, 1967, MIYAWAKI 1967). However, each grassland type has a range of ecological gradient. Grasslands belonging to the same *Zoysia* type are diversified with different degrees of succession. We usually classify the *Zoysia* type, the *Miscanthus* type, etc., but there are, in fact, transitional types between such main types which are especially continuous as ecological gradients as several authors mentioned (YOSHIDA 1950, SUZUKI & ABE 1959, NUMATA 1961). The location of various grasslands in the course of succession must be given by a certain quantitative measure. For this purpose, the author proposed the so-called degree of succession at the symposium "Succession in Japan" of the 25th General Meeting of the Botanical Society of Japan in 1960 (NUMATA 1961).

An ecological basis of judging grassland conditions and trends is to measure successional progression or retrogression quantitatively. The author has ever tried to judge grassland conditions and trends by the floristic composition (NUMATA 1965), the biological spectrum (NUMATA 1966), the spatial pattern of plant distribution (NUMATA & YODA 1957), the buried-seed population in the soil (NUMATA et al. 1964, NUMATA, AOKI & HAYASHI 1964, HAYASHI & NUMATA 1964, 1966), the moss indicator (NUMATA 1966), etc.

Besides the methods mentioned above, the author has applied DS (degree of succession) to judge the grassland condition and trend quantitatively. PICHI-SERMOLLI (1948) suggested an index for the establishment of the maturity in plant communities based on the frequency percent of all species in the stands of a community. This is an idea, however the author's DS is not only based on the frequency percent but various characteristics of plant communities. DS is defined as follows:

$$DS = [(\sum ld)/n] \times v$$

where l is the life span of the constituents, d is the dominance (for example, SDR [1]), n is the number of species, and v taking values from 0 to 1 is the vegetation cover as 100 % = 1 (NUMATA 1962). "l" is assumed as Th = 1, Ch, H and G = 10, N = 50, and M and MM = 100 according to life-forms. Such assumptions are based on the data of longevity of plants (MOLISCH 1938). According to the

[1]) SDR is a measure of relative importance of constituent species of a community expressed by the summation of ratios of phytosociological characteristics such as the two-factor SDR of $(C'+H')/2$ % where C' and H' are the cover ratio (%) and the hight ratio (%) respectively (NUMATA 1966).

idea mentioned above, the author applied DS to different types of grassland in Japan since 1961 (NUMATA 1961, 1962, 1963, 1964, 1965, 1966) and PARK (1965) to those in south Korea.

1) *Miscanthus sinensis* type grassland (the most representative high grass [1]) type meadow)

The *Miscanthus* type grasslands are most representative in mesic semi-natural grasslands (Tables II, III). Some of them are used for mowing (i.e. meadows) and others are mainly seral stages of

TABLE III

Floristic composition of a *Miscanthus sinensis* type grassland (No. 6611)

Species	SDR
Miscanthus sinensis ANDERS.	100
Lespedeza bicolor TURCZ. var. *japonica* NAKAI	60
Pteridium aquilinum KUHN	43
Hydrangea paniculata SIEB.	37
Aster scaber THUNB.	32
Eupatrium japonicum THUNB.	26
Astilbe odontophylla MIQ.	25
Lysimachia clethroides DUBY	23
Iris ensata THUNB. forma *spontanea* MAKINO	21
Hypericum erectum THUNB.	20
Inula salicina L. var. *asiatica* KITAM.	20
Artemisia japonica THUNB.	18
Potentilla Freyniana BORNM.	14
Carex lanceolata BOOTT	13
Petasites japonicus MAXIM.	13
Hosta undulata BAILEY var. *erromena* F. MAEKAWA	13
Desmodium racemosum DC.	13
Lastrea thelypteris BORY	10
Lespedeza pilosa SIEB. & ZUCC.	10
Agrimonia pilosa LEDEB.	10
Ixeris dentata MAKINO	10
Carex Maximowiczii MIQ.	9
Viola mandshurica W. BECKER	5
Polygonatum sacchalinense FR. SCHM.	5
Reynoutria japonica HOUTT.	4
Cirsium japonicum DC.	3

secondary succession. There are rare cases used for grazing, because the growing point of *Miscanthus sinensis* is rather high above the ground and its regenerative capacity is small. Therefore, even the mowing in the growing season gives strong effects against regenera-

[1]) HANSON (1962) defined high grass as a class of grasses, 6 to 8 feet high or more, compared with medium-hight grass and short grass.

TABLE IV

Characteristics of *Zoysia japonica* type grasslandss

Number	6119-b	6124-a	6125-b	6125-c
Location	Kaminokuni Hokkaido	Mountain-Farm Tottori Univ. Tottori Pref.	Nishino-hara Mt. Sambe, Shimane Pref.	Kitano-hara Mt. Sambe, Shimane Pref.
Use	Grazing	No use	Grazing	,,
Dominant	*Zoysia japonica*	,,	,,	,,
v	1.0	1.0	1.0	1.0
n	24	26	32	33
DS	200	870	456	345
SDR	57.5	59.1	54.0	63.9
SDR′	14.4	8.1	10.0	7.8
	6262	6267	6268	6278
	Sea coast, Shirahama-Chiba Pref.	Shinjukugyoen Park, Tokyo	,,	Mt. Dogo, Hiroshima Pref. 1200 m alt.
	No use	Exclosure	Weak trampling	Grazing
	Zoysia japonica	,,	,,	,,
	1.0	1.0	1.0	1.0
	16	8	6	7
	238	200	199	384
	56.7	78.6	75.0	100
	11.8	30.6	39.8	33.7

tion. People usually cut the above-ground part of *Miscanthus sinensis* after flowering in September or October.

Miscanthus sinensis is widely distributed from northern Hokkaido in the subarctic climate to Ryukyu Islands in the subtropical climate, though its forms or varieties extend the distribution to the southern Pacific islands. Its life-form is ChD_1R_3t with large bunches (NUMATA 1965). Parts of the aerial shoot overwinter with green body, though the upper part has already withered.

Windy places near the top of hills or mountains are often covered by high grass type or dwarf bamboo type grasslands notwithstanding forest climax zones (for example, No. 6438 in Table II).

The ground cover ratio of grassland vegetation (v) of the *Miscanthus* type is almost 1.0 and some degenerate phases show the ratios less than 1.0 as No. 6254, 6315, etc. in Table II. The number of species is 25 or thereabout, but is less than 25 in somewhat degrad-

6248	6256	6258	6259	6260
Yawata-Pasture, Nasu-machi Tochigi Pref.	Asama-Pasture, Gumma Pref.	,, (on lava)	,,	
,,	,,	,,	,,	After denudation
,,	,,	,,	,,	,,
1.0	1.0	1.0	1.0	0.2
29	46	63	59	13
235	312	228	332	239
52.7	100	85.0	74.3	58.8
13.2	12.4	8.8	6.8	23.0
6282	6283	6355	6110-a	6245
Chugoku-sanchi, " 1220 m alt.	Hakkoda, Aomori Pref.	Shizenkyoiku-en Park, Tokyo	Toimaki, Esashi, Hokkaido	Riverside Akan Kushiro, Hokkaido
,,	,,	Trampling	Grazing	No use
,,	,,	,,	Poa pratensis	,,
1.0	0.7	0.8	1.0	1.0
27	11	13	11	15
225	340	187	381	278
100	100	73.8	100	66.4
15.9	18.7	19.8	20.7	14.3

ed phases as No. 6277, 6315, 6321, 6326 etc. No. 6224 is a very special case which is the herbaceous layer of an *Acer Miyabei* forest. Since this forest was used for grazing, the herbaceous layer became the *Pteridium* type. A great number of species are shown in No. 6257 and 6261 which seem to be very heterogeneous and are excluded from the calculation. The summed dominance ratios (SDR) of the dominant, *Miscanthus sinensis* are mostly about 100. When SDR of *Miscanthus sinensis* is low as No. 6401, there are co-dominants competing with it, for example, shrubby species as *Lespedeza bicolor*. The relative SDR (SDR′) of *Miscanthus sinensis* to the total SDR values of a stand is usually 15 or so (sample mean: 16.5) nevertheless the SDR is nearly 100. When there are a lot of competing species with the dominant, SDR′ of the dominant becomes smaller as that of No. 6401, 6261, etc.

The distribution curve of the degree of succession (DS) of *Miscan-*

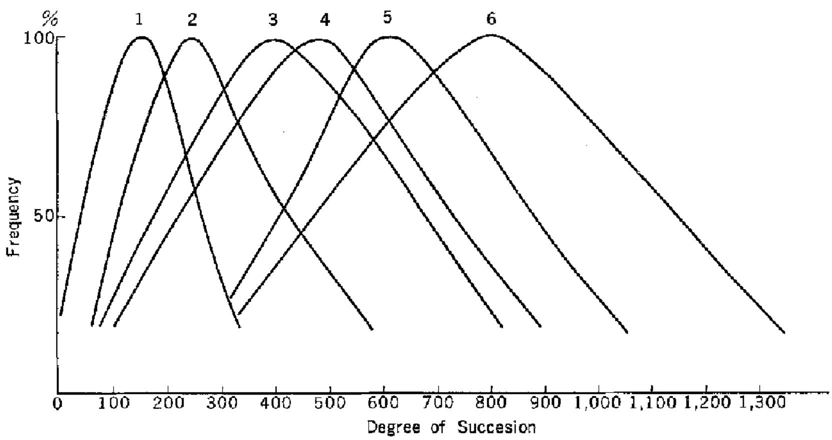

Fig. 4. The frequency curve of DS of grassland vegetation, i.e. the ordination of grassland types or stages by DS. 1: *Erigeron* stage, 2: *Zoysia japonica* stage, 3: *Pteridium aquilinum* stage, 4: *Miscanthus sinensis* stage, 5: *Pleioblastus* stage, 6: *Sasa* stage.

thus type grasslands seems to be a normal curve having the mode at about 400—500 in DS (sample mean: 435) and the range from 100 to 1000 (Fig. 4). Early stages of *Miscanthus* type grasslands show 100—200 of DS as No. 6257, 6276, 6326, and on the other hand, its advanced stages show 900—1000 at largest as No. 6224 which includes many saplings of trees like *Acer Miyabei*, *Quercus crispula*, etc.

2) *Zoysia japonica* type grassland (the most representative short grass type pasture)

The *Zoysia* type grasslands are the most representative type of pasture in Japan, especially in the cool-temperate climate (Tables IV, V). Species of *Zoysia* are distributed rather widely from the north-eastern part of Japan to south-Pacific islands, however *Zoysia japonica* dominates in the limited area in Japan, under biotic pressures as grazing and trampling (NUMATA 1961, SUGANUMA 1966, 1967). This species does not appear in the ordinary course (i.e. orthosere) of secondary succession. The life-form of *Zoysia japonica* is ChD_4R_1p with stolons or rhizomes (NUMATA 1966, NUMATA & ASANO 1968). This Japanese lawn grass is a northern vicariant genus corresponding to a tropical pasture grass, *Cynodon dactylon*. As mentioned above, OSEKO (1937) showed the representative course of grassland succession as waste stage ⇌ *Zoysia* stage ⇌ *Miscanthus* stage where the leftward direction indicated the strengthening of the biotic pressure. This scheme is the most usual plagiosere under the biotic pressure in the cool-temperate climate, but it gives place

TABLE V

Floristic composition of a *Zoysia japonica* type grassland (No. 6256)

Species	SDR
Zoysia japonica STEUD.	100
Kummerowia striata SCHINDL.	50
Metanarthecium luteo-viride MAXIM.	47
Rhododendron japonicum SURINGER	42
Trifolium repens L.	38
Miscanthus sinensis ANDERS.	37
Spiraea japonica L. fil.	34
Viola mandshurica W. BECKER	29
Sanguisorba officinalis L.	28
Arundinella hirta TANAKA	28
Agrostis clavata TRINIUS	27
Potentilla Freyniana BORNM.	26
Berberis Thunbergii DC.	24
Drosera rotundifolia L.	23
Carex nubigera D. DON subsp. *albata* T. KOYAMA	20
Geranium Thunbergii SIEB. & ZUCC.	18
Lactuca dentata MAKINO	16
Salix integra THUNB.	16
Fimbristylis tristachya R. BR. *var. subbispicata* T. KOYAMA	16
Cerastium glomeratum THUILL.	15
Malus Siebodii REHD.	13
Rosa multiflora THUNB.	12
Gentiana triflora PALL. var. *japonica* HARA	11
Cirsium Tanakae MATSUM.	11
Plantago camtschatica CHAMISSO	10
Patrinia villosa JUSS.	10
Spiranthes sinensis AMES	8
Carex nervata FRANCH. & SAV.	8

to the course of annual stage ⇌ *Pleioblastus* stage ⇌ *Miscanthus* stage in the warm-temperate climate (NUMATA 1961, 1965).

The northern limit of the *Zoysia* type pasture is verified to be southern Hokkaido including the Oshima Peninsula and the Erimo Cape. No. 6119-b in Table IV shows an example of such a northern pasture. But the most part of Hokkaido except southern Hokkaido mentioned above is covered with the *Poa pratensis* type pasture instead of the *Zoysia* type pasture (No. 6110-a, 6245). The *Zoysia* type pasture of No. 6283 (Table IV) is located in the centre of distribution of the species and of No. 6278 shows the same type pasture established in the *Fagus crenata* zone altitudinally.

The ground cover ratio (v) of the *Zoysia* type grasslands is almost 1.0 and some deteriorated phases by strong grazing or trampling show the ratios less than 1.0 as No. 6283 and 6355. SDR of *Zoysia japonica* has wide ranges from 50 to 100 though it dominates in all of those stands. Its dominancy is more variable than that of

TABLE VI

Characteristics of *Pleioblastus* type grasslands

Number	6120-a	6249	6251	6274	6517	6518	6519
Location	Konda-machi Hyogo Pref.	Minamiga-oka Nasu-machi Tochigi Pref.	Furukome, Narita-shi Chiba Pref.	Shinodayama Wakayama Pref.	Taikanbo, Mt. Aso, Kumamoto Pref.	,,	Nishiozono Kuju-machi Oita Pref.
Use	No use	Weak grazing	Tethering	No use	Mowing	Biennial mowing	Grazing
Dominant	*Pleioblastus distichus* var. *nezasa*	*Pleioblastus Chino*	,,	*P. distichus* var. *nezasa*	,,	,,	,,
v	1.0	1.0	1.0	1.0	1.0	1.0	1.0
n	17	41	22	16	14	11	16
DS	898	554	418	557	614	848	470
SDR	76.2	91.7	83.3	92.2	100	93.5	82.0
SDR	13.5	9.4	14.6	6.3	19.6	24.7	15.0

	6520	6521-a	6521-b	6525	6526	6527	6625
	Kokonoe-machi Oita Pref.	South mouth of mount., Mt. Kuju, Oita Pref.	,,	Handa-kogen Oita, Pref.	Amagaike Pass Mt. Kuju, Oita Pref.	Bogatsuru, Mt Kuju, Oita Pref.	Pref. Forest, Narita-shi, Chiba Pref.
	Grazing	,,	,,	Strong grazing	No use	Overgrazing	No use
	P. distichus var. *nezasa*	,,	,,	,,	,,	,,	*P. Chino*
	1.0	1.0	0.9	1.0	1.0	1.0	0.9
	20	17	17	30	28	16	18
	578	665	580	466	494	617	913
	88.5	91.4	70.0	67.0	75.0	63.0	100
	14.2	12.3	19.3	8.4	13.0	21.5	21.2

Miscanthus sinensis. The number of species is also very variable from 6 to 63 with a sample mean of 24, but the homogeneous *Zoysia* pasture of good quality seems to have small number of species as No. 6278, 6283, etc. SDR′ of *Zoysia japonica* is 15 or so (sample mean: 17.4) similar to that of *Miscanthus sinensis*. The distribution curve of DS shows its range from 100 to 500 with the mode of 250 (sample mean: 237), except No. 6124-a having a co-dominant of *Pleioblastus distichus* var. *nezasa*.

3) *Pleioblastus distichus* var. *nezasa* type grassland (the most representative grazing land in south-western Japan).

Regarding the dwarf-bamboo type grassland, the author ever tried to give its orientation in the grassland types in Japan (NUMATA 1961, 1963, 1965). The dwarf-bamboo type grasslands are divided into two main classes, viz. the *Sasa* type meadow which distributes in the subarctic and cool-temperate regions and the *Pleioblastus* type

TABLE VII

Floristic composition of a *Pleioblastus* type grassland (No. 6521-b)

Species	SDR
Pleioblastus distichus MUROI & H. OKAM. var. *nezasa* MUROI	70
Miscanthus sinensis ANDERS.	59
Salix subopposita MIQ.	28
Pteridium aquilinum KUHN	27
Lespedeza cyrtobotrya MIQ.	25
Cymbopogon Goeringii HONDA	24
Angelica longeradiata KITAG.	22
Salix Saidaeana SEEMEN	18
Artemisia vulgaris L. var. *indica* MAXIM.	17
Haloragis micrantha R. BR.	14
Lysimachia clethroides DUBY	14
Carex nervata FRANCH. & SAV.	12
Agrostis clavata TRINIUS	10
Sanguisorba officinalis L.	10
Pinus densiflora SIEB. & ZUCC.	7
Polygala japonica HOUTT.	4
Viola pumila W. BECKER	2

pasture or meadow in the warm-temperate region (Tables VI, VII). OSEKO (1937) recognized the *Sasa* stage in the grassland succession, but he confounded the *Pleioblastus* stage with the *Sasa* stage. According to MAEKAWA (1960), the genera of dwarf-bamboos in Japan are classified into large groups of *Sasa* and *Pleioblastus* and their intermediate type, *Sasaella* is very akin to *Arundinaria* keeping an ancestral form of dwarf-bamboos.

The author did not see the dwarf-bamboo type pasture in the Nepal Himalaya, but *Arundinaria* is very often seen as a shrubby layer

TABLE VIII

Characteristics of *Sasa* type grasslands

Number	6209	6212	6213	6214	6218
Location	Iwaobetsu, Shari-machi Hokkaido	,,	,,	,,	,,
Use	No use	Weak grazing, Undergrowth of *Quercus crispula* stand	Strong grazing	No use, burnt site	Very strong grazing
Dominant	*Sasa veitchii*	,,	,,	,,	,,
v	1.0	1.0	0.3	1.0	0.4
n	7	9	12	22	10
DS	1154	1841	378	955	289
SDR	100	91.7	100	76.6	50.0
SDR′	32.5	34.8	29.3	10.0	17.2

Number	6232	6233	6303	6304	6310	6322
Location	Rikushibetsu, Rausumura, Hokkaido	Samui, Shibetsumachi, Hokkaido	Kamishihoro Hokkaido (720 m alt.)	,,	Shihoromura, Hokkaido (570 m alt.)	Kawatabi, Narugo-machi Miyagi Pref.
Use	No use, burnt site	Weak grazing	Strong grazing	Weak grazing	,,	,,
Dominant	*Sasa veitchii*	,,	,,	,,	*Sasa nipponica*	*Sasa paniculata*
v	1.0	1.0	0.5	0.95	1.0	0.9
n	9	21	7	7	12	25
DS	1401	554	455	815	603	657
SDR	84.8	61.5	76.9	90.9	63.3	64.2
SDR′	23.6	11.2	34.9	34.9	20.5	11.0

6219	6221	6225	6226	6227
,,	,,	Horobetsu, Shari-machi, Hokkaido	,,	,,
,,	Weak grazing, undergrowth of *Quercus dentata* stand	Grazing, under-growth of *Acer Miyabei* stand	No use, ,,	Mowing, felled site
,,	,,	,,	,,	,,
0.3 13 203 90.0 18.0	0.8 5 1275 87.5 43.3	0.9 10 1177 100 39.7	1.0 9 3197 91.7 30.6	1.0 14 1044 87.5 14.0

6425	6437	6440	6442	6444
Yabitsu-Pass, Mt. Tanzawa, Kanagawa Pref.	Okoeji, ,,	Mt. Omuro, Kanagawa Pref.	Mt. Sodehira ,,	Himetsugu, Mt. Tanzawa Kanagawa Pref.
No use	,,	,,	,,	,,
Sasa borealis	,,	,,	,,	*Sasa hayatae*
1.0 11 1210 86.0 29.5	1.0 20 935 84.3 14.7	1.0 16 945 100 21.1	0.9 28 914 65.0 10.4	1.0 15 498 71.8 14.2

under the forest canopy. The leaves of *Arundinaria* are used for forage (NUMATA 1965, 1967). The species of *Arundinaria* cover wide areas of lowland and mountain region in Nepal and neighbouring countries. These seem to be distributed widely as ancestral forms as well as in North and South America and Africa. The author sometimes saw *Arundinaria* grasslands in central Brazil (NUMATA 1967).

Meanwhile, in Japan, *Sasaella* covers very small area in the point of contact of *Sasa* and *Pleioblastus* (i.e. in the vicinity of Mt. Hakone, etc.). Therefore the dwarf-bamboo type grasslands in Japan are classified broadly into two zones of *Sasa* type and *Pleioblastus* type. The *Sasa* type grasslands are seral stages of the subarctic *Picea jezoensis-Abies sachalinensis* zone and of the cool-temperate *Fagus crenata* zone, and the *Pleioblastus* type grasslands are those of the *Shiia Sieboldii*, evergreen *Quercus* zone.

Among the species of *Pleioblastus*, *Pleioblastus Chino* distributes mainly from Kanto (northern part of warm-temperate region) to Tohoku (cool-temperate region). The *Zoysia* type pasture takes the place of the *Pleioblastus Chino* or *Sasaella ramosa* type grassland according to grazing in the cool-temperate region. The author confirmed this fact at the Kozu Pasture, Gumma Prefecture (NUMATA 1967). However, the same *Pleioblastus Chino* type grassland deteriorates to the annual type grassland dominated by *Polygonum Blumei*, *Digitaria adscendens*, *Microstegium vimineum*, etc. in the warm-temperate lowlands.

The ground cover ratio (v) of the *Pleioblastus distichus* var. *nezasa* type pastures or meadows shows usually 1.0. *Pleioblastus distichus* var. *nezasa* lowers its height under strong grazing pressure, but hardly denudes its ground cover, in spite of overgrazing, while *Pleioblastus Chino* is weak against the grazing pressure and its grassland moves back to the annual type pioneer stage (cf. No. 6626, 6627 in Table VI). SDR of *Pleioblastus distichus* var. *nezasa* is high under mowing or no use because its height as well as cover is great. SDR of *Pleioblastus distichus* var. *nezasa* is considerably high even under grazing except under overgrazing as No. 6525 and 6527. The number of species is twenty or thereabout (sample mean: 20.4) with the exception of No. 6249 of *Pleioblastus Chino*, etc. SDR′ of *Pleioblastus* spp. is 15 or so (sample mean: 14.9), in general, similar to that of *Miscanthus sinensis* or *Zoysia japonia*. The distribution curve of DS shows its range from 400 to 1000, with the mode of about 600 (sample mean: 622).

4) *Sasa* type grassland (northern forest-pasture, pasture or meadow, especially in Hokkaido)

The dominants of dwarf-bamboo type pastures mainly in Hokkaido are *Sasa nipponica* and *Sasa veitchii* (Tables VIII, IX). Especially the latter covers a very wide area. The *Sasa veitchii* grassland established after burning or felling forests keeps a rather constant state when it is used properly for mowing, but degenerates under grazing. In north-eastern Hokkaido, the artificial pasture composed of forage grasses and legumes introduced from northern or middle Europe is easily established through dungs of cattle or artificial seeding after withering of *Sasa* or denudation by overgrazing. This forage type pasture as No. 6110-a in Table IV is kept permanently only in Hokkaido with a balance to proper grazing. The deteriorated *Sasa* type pasture by overgrazing may progress to *Betula platyphylla* var. *japonica*-, *Quercus crispula*-, *Quercus mongolica*-forests.

TABLE IX

Floristic composition of a *Sasa* type grassland (No. 6227)

Species	SDR
Sasa veitchii REHD.	88
Miscanthus sinensis ANDERS.	73
Pteridium aquilinum KUHN	72
Petasites japonicus MAXIM. var. *giganteus* HORT.	62
Cacalia hastata L. var. *glabra* LEDEB.	51
Phleum pratense L.	51
Artemisia montana PAMP.	45
Acer Miyabei MAXIM.	39
Salix Bakko KIMURA	35
Anaphalis margaritacea BENTH. & HOOK. fil.	35
Hypericum erectum THUNB.	34
Eupatrium sacchalinense MAKINO	32
Taraxacum officinale WEBER	4
Viola verecunda A. GRAY	3

There is another case going forth to the *Pteridium aquilinum* type grassland by overgrazing. Because *Pteridium aquilinum* is unpalatable for cattle and horse, its dominancy increases rapidly under such a selective grazing.

YOSHIDA (1950) reviewed the successional sequence in grassland by OSEKO (1937) pointed out the *Sasa* stage as a representative pasture in Japan, but this is one of dwarf-bamboo type pastures including the *Pleioblastus* stage. We must distinguish the *Pleioblastus* type from the *Sasa* type in spite of the same dwarf-bamboo type grasslands as already mentioned. YOSHIDA (1956) also pointed out the successional course of the *Sasa* stage → the *Miscanthus* stage under proper use and the *Miscanthus* stage → the *Sasa* stage → the *Zoysia* stage, or the *Miscanthus* stage → the *Zoysia* stage under excessive use. However the competition of *Miscanthus* versus *Sasa* is affected by climatic conditions as well as biotic interference as above, and the

TABLE X

Characteristics of *Pteridium aquilinum* type grassland

Number	6112-a	6112-b	6112-c	6129-a	6129-b	6210	6217
Location	Motoineppu, Omu-machi, Hokkaido	,,	,,	City-forest Sapporo, Hokkaido	,, ,,	Iwaobetsu, Shari-machi, Hokkaido	,, ,,
Use	No use	,,	,,	After felling	,,	Grazing	Overgrazing
Dominant	*Pteridium aquilinum*	,,	,,	*Pteridium aquilinum*	,,	,,	,,
v	1.0	1.0	1.0	0.8	1.0	1.0	0.7
n	12	11	8	9	16	17	14
DS	343	1197	397	420	202	731	365
SDR	100	61.0	100	85.0	100	100	85.0
SDR′	35.6	27.0	57.7	30.0	27.1	29.3	20.2

TABLE XI

Floristic composition of a *Pteridium aquilinum* type grassland (No. 6323)

Species	SDR
Pteridium aquilinum KUHN	100
Hydrocotyle ramiflora MAXIM.	46
Zoysia japonica STEUD.	43
Lactuca dentata MAKINO	22
Miscanthus sinensis ANDERS.	22
Dryopteris Thelypteris A. GRAY	21
Rubus parvifolius L.	16
Trifolium repens L.	16

6115-b	6125-a	6127-a	6127-b	6127-c
Kami-mobetsu, Hokkaido	Higashinohara Mt. Sanbe, Shimane Pref.	City-forest, Sapporo, Hokkaido	,,	,,
Grazing	,,	No use	,,	,,
,,	,,	,,	,,	,,
1.0 18 625 100 29.4	1.0 41 486 93.4 8.7	1.0 19 633 100 19.5	1.0 22 343 63.5 23.6	1.0 22 275 61.6 27.9

6223	6234	6241	6306	6323
Horobetsu, Shari-machi, Hokkaido	Saimu, Shibetsu-machi Hokkaido	Nokke Peninsula, Hokkaido	Kami-shihoro, Hokkaido	Kawatabi, Miyagi Pref.
,,	Weak grazing	Grazing	After burning	Grazing
,,	,,	,,	,,	,,
1.0 17 281 75.0 33.4	1.0 18 768 81.3 13.7	1.0 22 318 100 13.2	0.85 9 396 93.3 23.7	0.95 15 278 100 28.6

Table XI (*continued*)

Species	SDR
Lycopus Maakianus MAKINO	15
Patrinia scabiosaefolia LINK	15
Lespedeza cuneata G. DON	15
Carex lanceolata BOOTT	15
Haloragis micrantha R. BR.	11
Potentilla Freyniana BORNM.	11
Prunella vulgaris L.	8

competing power of *Miscanthus sinensis* is, in general, too weakened in north-eastern Hokkaido to make a homogeneous grassland dominated by the species. Therefore the coactive relation of *Miscanthus* to *Sasa* is different in the subarctic and cool-temperate regions.

The ground cover ratio (v) of the *Sasa* type pasture is about 1.0 under weak grazing, but lowers to 0.3 or 0.4 under strong grazing as No. 6213, 6218, 6219, etc. The number of species has a wide range from 5 to 28 with a sample mean 13.4. But it is rather small compared with other types of grassland, because the dominancy of *Sasa* is very great. The dominancy of *Sasa* lowers through grazing or other causes like No. 6218, 6233, 6310, etc., but, in general, SDR of *Sasa* is from 80 to 100, and SDR 'has a wide range from 10 to 40. The typical dominancy of *Sasa* is 100 in SDR and 30 in SDR' which is rather high compared with other types of grassland mentioned above. DS has a very wide range from 200 to 3000 whose high values belong to the undergrowth type as No. 6212, 6221, 6225, 6226, etc.

DS from 200 to 500 is of very strong grazing and that over 1000 is mainly of undergrowth of the forest stand. If the *Sasa* type as the undergrowth of forest stand is excluded, the mode of the frequency curve of DS may be about 800.

5) *Pteridium* type grassland

Pteridium aquilinum is very widely distributed in Japanese grasslands, but this grassland type dominated by *Pteridium aquilinum* is a deteriorated one by grazing or burning. Especially the fresh plants of *Pteridium aquilinum* are poisonous by their anti-B_1 enzymatic action, but this bracken is used for mowing in a part of the Tohoku District (Aomori Prefecture) as a solitary exception. These aerial shoots of *Pteridium* are used for forage mixed with rice-bran. *Pteridium* is noticed particularly in short grass type pastures dominated by *Zoysia japonica* or *Pleioblastus distichus* var. *nezasa* and people sometimes call them the *Pteridium* type physiognomically. However, *Pteridium aquilinum* is not always dominant in SDR. SUZUKI & ABE (1959) reported the similar specific correlation (spezifische Massengemeinschaftskoeffizient) of *Pteridium aquilinum* with *Miscanthus sinensis* and *Pleioblastus distichus* var. *nezasa*. At any rate, the *Pteridium* type grassland has a character of the transitional type. OSEKO (1937) supposed the *Pteridium* type as a seral stage corresponding to the soil fertility of the *Lespedeza*- and *Sasa* stages between the waste (probably annual) stage and the forest stage.

However, according tho the author's study (Tables X, XI), the mode of DS of the *Pteridium* stage is about 400 between the *Zoysia* stage and the *Miscanthus* stage. The ground cover ratio (v) of the *Pteridium* type grassland is almost 1.0 and the number of species is twenty or so with a range from 9 to 41. SDR is from 60 to 100 and SDR′ is mostly from 20 to 30 with a wide range from 10 to 60. The case of SDR′: 57.7 (No. 6112-c) is a special one which *Pteridium aquilinum* dominates in the *Poa pratensis* type pasture. The case of SDR′: 8.7 (No. 6125-a) is also a special one with many species. DS has a wide range from 200 to 1200 with the mode of about 400. The case of DS: 1197 (No. 6112-b) is a very special, transitional stage approaching to the *Betula platyphylla* var. *japonica* stage (the pioneer arborescent stage in the northern half of Japan). If this special case is excluded, the range of DS is from 200 to 800 with a narrower range than that of the *Miscanthus* type meadow.

6) Deteriorated stages dominated by *Erigeron* spp. etc.

As the dominants of pioneer stages in the secondary succession in Japan, *Ambrosia artemisiifolia*, *Digitaria adscendens*, *Erigeron annuus*, *E. canadensis*, *Polygonum Blumei*, *P. Persicaria*, *Setaria viridis*, etc. are noticeable. Pioneer stages in general are not dealt with here, but only initial stages after felling, denudation of turf, tethering, trampling, over-grazing, etc. are discussed. This type was called the "waste type" by OSEKO (1937). In the examples of Tables XII, XIII, the ground cover is usually smaller than 1.0 and the number of species is 15 or 20 with a range from 7 to 34. SDR is from 60 to 100 and SDR′ is from 10.8 to 36.9. SDR′ of the dominant is larger, in general, in a community composed of smaller number of species and smaller in the reverse case. A greater SDR′ of the dominant with smaller n as in No. 6129-b, 6121-b, 6110-b, and 6313 shows an overwhelming predominance of such dominants as *Erigeron canadensis*, *Digitaria adscendens*, *Rumex obtusifolius*, *Agrostis palustris*, etc. Some of the dominants in the deteriorated stage are common to pioneer species in the old-field succession as *Digitaria adscendens*, *Erigeron canadensis*, *E. annuus*, *E. sumatrensis*, *Polygonum Blumei*, *P. nodosum* etc., but others are different as *Poa annua*, *Plantago asiatica*, *Paspalum Thunbergii*, *Rumex obtusifolius*, *Trifolium repens*, *Glysine soja*, *Agrostis palustris*, etc. Some of the latter are trampling plants. DS covers a range from 70 to 253 with the mode of about 150, which is rather high compared with that of pioneer stages of old-field succession, because deteriorated stages of grassland have usually many perennial species. For example, the values of DS of the *Polygonum Persicaria* stage and the *Erigeron* stages in a normal old-field succession are 64.4 and 127.5 respectively (HAYASHI 1967).

There are various minor types of grasslands besides the main types as mentioned above. For instance, dominants of such minor types are grassy type with *Arundinella hirta*, *Imperata cylindrica* var. *Koenigii*, *Ischaemum anthroides*, *Calamagrostis hakonensis*, *C. Epigeios*, *Hakonechloa macra*, etc.; sedge type with *Carex leucochloa*, etc.; forb type with

TABLE XII

Characteristics of deteriorated grasslands dominated by *Erigeron* spp. etc.

Number	6110-b	6112-d	6115-c	6121-b	6124-b	6126-b
Location	Toimaki, Esashi-machi, Hokkaido	Omu-machi, Hokkaido	Kamimobetsu, Hokkaido	Konda-machi, Hyogo Pref.	Mountain Farm Tottori Univ. Tottori Pref.	Chojabar Chugoku Exp. Sta. Ota-shi, Shimane
Use	Horse resting place	Overgrazing	Cattle resting place	Tethering	After denudation of turf	No use
Dominant	*Rumex obtusifolius*	*Poa annua*	*Trifolium repens*	*Digitaria adscendens*	*Paspalum Thunbergii*	*Erigeron sumatrensi.*
v	0.4	0.15	0.2	0.6	0.5	1.0
n	8	11	10	7	21	14
D	101	61	80	239	113	70
SDR	100	75.0	60.0	100	61.3	88.4
SDR′	36.9	16.7	14.2	33.7	10.8	19.0

Number	6305	6309	6311	6313	6324	6325
Location	Kamishihoro, Hokkaido	Shihoro-mura Hokkaido	,,	,,	Tashiro, Kawatabi, Miyagi Pref.	Kawatab Miyagi P
Use	Overgrazing	Horse resting place	Overgrazing	Abandoned farmland	Cattle resting place	Abandon farmland
Dominant	*Polygonum nodosum*	*Plantago asiatica*	*Agrostis palustris*	,,	*Poa annua*	*Agrostis palustris*
v	0.3	0.5	0.5	0.9	0.3	1.0
n	10	20	20	8	10	25
D	142	253	135	208	71	172
SDR	91.6	63.3	78.6	60.6	62.7	86.3
SDR′	20.7	11.8	14.3	31.3	20.0	13.8

6129-b	6201	6205	6206	6216	6229	6269
City Forest Sapporo, Hokkaido	Aoyama, Ikeda-machi Hokkaido	Iwaobetsu, Shari-machi Hokkaido	,,	Mumeiko, Iwaobetsu, Shari-machi, Hokkaido	Utoro, Hokkaido	Shinj Park, Toky
After felling	Horse resting place	Tethering	,,	Abandoned farmland	Horse tethering	Tram
Erigeron canadensis	*Erigeron annuus*	*Trifolium repens*	,,	*Erigeron canadensis*	*Agrostis palustris*	*Poa a*
0.7	0.4	0.8	0.4	1.0	0.8	0.8
16	25	12	8	17	16	8
141	184	176	176	206	190	118
100	66.6	61.7	60.0	100	82.2	75.0
27.1	13.6	16.2	21.2	8.8	17.4	26.6

6327	6331	6349	6434	6445	6626	6627
,,	Ichinomiya, Chiba Pref.	Kogasaki, Matsudo, Chiba Pref.	Kinomatagoya, Mt. Tanzawa, Kanagawa Pref.	Himetsugu Mt. Tanzawa ,,	Pref. Forest, Narita-shi, Chiba Pref.	Furuk Narit ,,
,,	Abandoned pasture	,,	Trampling	,,	Grazing	Cattl tether
Echinochloa Crus-galli	*Erigeron annuus*	*Glysine soja*	*Plantago asiatica*	,,	*Polygonum Blumei*	*Digita adscen*
1.0	1.0	1.0	0.9	0.8	0.7	0.9
21	27	34	13	15	27	19
140	252	97	231	217	224	136
98.0	96.8	94.5	63.6	83.3	67.0	68.0
14.1	20.0	15.9	17.6	21.9	10.6	11.8

Thalictrum Thunbergii, *Artemisia vulgaris* var. *indica*, *A. vulgaris* var. *vulgatissima*, *Lotus corniculatus* var. *japonicus*, *Comanthosphace sublanceolata* f. *hakonensis*; fern type with *Osmunda cinnamomea*; and shrubby type with *Lespedeza bicolor*, *L. bicolor* var. *japonica*, etc. Ecological orientation of these minor types will be given by applying a general principle for the main types as stated above.

TABLE XIII

Floristic composition of an *Erigeron* type grassland (No. 6126)

Species	SDR
Erigeron sumatrensis RETZ.	88
Artemisia vulgaris L. var. *indica* MAXIM.	65
Erigeron annuus PERS.	55
Erigeron canadensis L.	45
Dactylis glomerata L.	35
Rhus javanica L.	34
Agrostis palustris HUDSON	33
Miscanthus sinensis ANDERS.	27
Rubus crataegifolius BUNGE	26
Setaria viridis BEAUV.	25
Siegesbeckia pubescens MAKINO	10
Trifolium repens L.	9
Cassia mimosoides L. var. *nomame* MAKINO	8
Hypericum erectum THUNB.	6

SUMMARY

The types of grassland vegetation expressed by the dominants were surveyed from north to south in Japan, and their successional and climatic relationships were given from the viewpoint of quantitative and dynamic ecology (Table I, Figs. 1—3).

There are many grassland types in Japan, but only major types were dealt with, compared by some characteristics (location, use, dominant, ground cover of vegetation (v), number of constituent species (n), degree of succession (DS), summed dominance ratio (SDR), and relative SDR (SDR′) and showing each example of the floristic composition (Tables II—XIII).

The grassland vegetation in Japan is not the climatic climax but seral stages, except alpine grasslands over the tree line of high mountains. There are two cases in grassland succession, orthosere and plagiosere. "Orthosere" is the ordinary subsere in the abandoned field lacking biotic suppressions, however "plagiosere" is the gradient under biotic pressures such as grazing, mowing, burning, etc. The latter is mostly dealt with in this paper.

The ordination of various grassland types in the DS-frequency relationships is given in Fig. 4. This is not a real course of the grassland succession, but ecological gradient of grassland types. Such an ordination of grassland vegetation in a given area may show the seral status itself.

ZUSAMMENFASSUNG

Der Verfasser hat die Typen der durch Dominanten gekennzeichneten Grünland-Vegetation von Norden bis Süden in Japan untersucht; Tab. I und die Abb. 1—3 geben die Sukzessions- und Klima-Verhältnisse von dem Gesichtspunkt der quantitativen und dynamischen Ökologie wieder.

Es gibt sehr viele Grünlandtypen in Japan, aber der Verfasser behandelt nur die größeren Typen im Vergleich zueinander durch einige Merkmale (Stellen, Gebrauch, Dominantarten, Vegetationsdeckungsgrad (v), Artenzahl (n), Sukzessionsgrad (DS), summierende Dominanz Verhältnisse (SDR), relative SDR (SDR')), und einige Beispiele der Artenzusammensetzung (Tab II—XIII).

Die japanische Grünland-Vegetation ist kein klimatischer Klimax, sondern serale Stufe, mit Ausnahme der alpinen Grünland-Vegetation über der Baumgrenze des Hochgebirges. Wir haben zwei Fälle in Grünland-Sukzessionen, Orthosere und Plagiosere. "Orthosere" ist die gewöhnliche sekundäre Sere auf dem verlassenen Feld ohne biotischen Druck, "Plagiosere" ist das Gefälle unter biotischem Druck, zum Beispiel, Weide, Mahd, Brand, usw. Der Verfasser behandelt hauptsächlich den letzteren Fall in dem Artikel.

Abb. 4 zeigt die Anordnung der verscheidenen Grünlandtypen auf die Verhältnisse der DS zur Frequenz. Das ist nicht ein wahrhaftes Fortschreiten der Grünland-Sukzession, sondern ein ökologisches Gefälle der Grünlandtypen. Solche Anordnung der Grünland-Vegetation einer gewissen Fläche wird den seralen Zustand selbst zeigen.

REFERENCES

Agricultural Research Council of the Ministry of Agriculture and Forestry, 1959 — Methods of surveying and measuring the semi-natural grassland vegetation, 66 pp. (Jap.).

Critchfield, W. B. & Little, Jr, E. L. 1966 — Geographic distribution of the pines of the world. *Miscel. Pub.* 991, Forest Service, U.S.D.A.

Hanson, H. C. 1962 — Dictionary of ecology. New York.

Hayashi, I. 1967 — Studies on the plant succession in Sugadaira, central Japan, 1. *Res. Rep. Sugadaira Bol. Expt. Sta.* 1: 1—18.

Hayashi, I. & Numata, M. 1964 — Ecological studies on the buried-seed population in the soil from the viewpoint of plant succession, III. *Physiol. Ecol.* 12, 1/2: 185—190. (Jap./Engl.).

HAYASHI, I. & NUMATA, M. 1966 — Ecological studies on the buried-seed population in the soil as related to plant succession, IV. From overmature pine forest to *Shiia Sieboldii* climax forest (preliminary report). *Ecol. Stud. Biotic Comm. Nat. Park Nat. Study*, 1: 62—71.
HAYASHI, I. & NUMATA, M. 1967 — Ecology of pioneer species of early stages in secondary succession, I. *Bot. Mag. Tokyo*, 80, 942: 11—22.
HONDA, S. 1900 — On the forest zones of Japan. Tokyo (Jap.).
ITOW, S. 1968 — Floristic composition of semi-natural grasslands in northwestern Kyushu (unpublished).
KAWANABE, S. 1956 — The climatic adaptation of northern type perennial forage crops. *Anim. Husband.* 10: 1011—1016. (Jap.).
KAWANABE, S. 1957 — Summer depression and cultural limit of perennial forage crops. *Ibid.* 11: 132—138. (Jap.).
MAEKAWA, F. 1960 — Evolutional aspects to the inter-generic or inter-specific hybrids. OKA, H. ed.: Reports of centennial meeting for Darwinism, 115—124. (Jap.).
McCLOUD, D. E. & MOTT, G. O. 1953 — Influence of association upon the forage yield of legume-grass mixtures. *Agron. J.* 45, 2: 61—65.
MIYAWAKI, A. ed. 1967 — Vegetation of Japan compared with other regions of the world. *Encyclop. Sci. Technol.*, Vol. 3 (Jap.).
MIYAWAKI, A. & ITOW, S. 1966 — Phytosociological approach to the conservation of nature and natural resources in Japan. Paper presented at Divisional Meeting of Conservation, *11th Pacific Sci. Congr.*, Tokyo.
MOLISCH, H. 1938 — The longevity of plants. New York.
NUMATA, M. 1954 — Some special aspects of the structural analysis of plant communities. *J. Coll. Arts Sci.*, Chiba Univ. 1, 4: 194—202.
NUMATA, M. 1956 — The developmental process of weed communities. Experimental studies on early stages of a secondary succession, II. *Jap. J. Ecol.* 6, 2: 62—66, 6, 3: 89—93 (Jap./Eng.).
NUMATA, M. 1961 — Ecology of grasslands in Japan. *J. Coll. Arts Sci.*, Chiba Univ. 3, 3: 327—342.
NUMATA, M. 1961 — Some problems in the secondary succession and judging the seral condition and trend. *Biol. Sci.* 13, 4: 146—152. (Jap.).
NUMATA, M. 1961 — Statistical methodology in plant ecology. *Bull. Int. Stat. Inst.* 38 (Part 4): 547—553.
NUMATA, M. 1962 — Judging grassland vegetation by degree of succession and index of grassland condition. *Kagaku* 32, 12: 658—659. (Jap.).
NUMATA, M. 1961—1963 — Studies on judging grassland conditions, I—III. (Jap.).
NUMATA, M. 1963 — *Sasa* type pastures in Japan. *Rep. Fuji Bamboo Garden* 7: 123—128. (Jap.).
NUMATA, M. 1965 — Ecological judgement of grassland condition and trend, I. Judgement by biological spectra. *J. Jap. Soc. Grassl. Sci.* 11, 1: 20—33. (Jap./Eng.).
NUMATA, M. 1965 — Ecological studies of dwarf-bamboo type grassland in Japan. *Bull. Grassl. Ecol. Res. Group* 6: 4—16. (Jap.).
NUMATA, M. 1965 — Grassland vegetation in eastern Nepal. *Ecol. Stat. Mount. Mt. Numbur in East. Nepal*, 74—94 (Jap./Eng.).
NUMATA, M. 1966 — Ecological judgement of grassland condition and trend, II. Judgement by floristic composition. *J. Jap. Soc. Grassl. Sci.* 12, 1: 29—36. (Jap./Eng.).
NUMATA, M. 1966 — Mosses as ecological indicator of grassland succession. *Misc. Bryol. Lich.* 4, 2: 13—16. (Jap.).
NUMATA, M. 1964—1966 — Studies on grassland productivity, I—III. (Jap.)
NUMATA, M. 1966 — Vegetation and conservation in eastern Nepal. *J. Coll. Arts Sci.*, Chiba Univ. 4, 4: 559—569.

NUMATA, M. 1966 — Northern *Pleioblastus* type grassland in Japan, particularly related to autecology of *Pleioblastus Chino* MAKINO. *Rep. Fuji Bamboo Garden* 11: 59—65 (Jap.).

NUMATA, M. 1966 — Some remarks on the method of measuring vegetation. *Bull. Marine Lab.*, Chiba Univ. 8: 71—78.

NUMATA, M. 1967 — Bamboos in Brazil. *Bamboo* 6: 55—58. (Jap.).

NUMATA, M., AOKI, K. & HAYASHI, I. 1964 — Ecological studies on the buried-seed population in the soil as related to plant succession, II. Particularly on the pioneer stage dominated by *Ambrosia elatior*. *Ibid.* 14, 6: 224—227. (Jap./Eng.).

NUMATA, M. & ASANO, S. 1968 — Biological Flora of Japan, Vol. I. Tokyo. (Jap./Eng.).

OHGA, N. & NUMATA, M. 1965 — Ecological analysis of successional development from herbaceous stage to arborescent stage, I. Establishment of *Pinus Thunbergii* stand. *J. Coll. Arts Sci.*, Chiba Univ. 4, 3: 263—275. (Jap./Eng.).

NUMATA, M., HAYASHI, I., KOMURA, T. & OKI, K. 1964 — Ecological studies on the buried-seed population in the soil as related to plant succession. I. *Jap. J. Ecol.* 14, 5: 207—215. (Jap./Eng.).

NUMATA, M. & SUZUKI, K. 1958 — Experimental studies on early stages of secondary succession. *Jap. J. Ecol.* 8, 2: 68—75. (Jap./Eng.).

NUMATA, M. & YAMAI, H. 1955 — The developmental process of weed communities. Experimental studies on early stages of a secondary succession, I. *Jap. J. Ecol.* 4, 4: 166—171. (Jap./Eng.).

NUMATA, M. & YODA, K. 1957 — The community structure and succession of artificial grasslands. I. *J. Jap. Soc. Herb. Crops Grassl. Farm.* 3: 4—11 (Jap./Eng.).

OSEKO, M. 1937 — Studies on the grasslands in Japan, Tokyo. (Jap.).

PARK, B. K. 1965 — Ecological studies on native grassland vegetation in Korea. *J. Kor. Cult. Res. Inst.* 5: 177—193.

PICHI-SERMOLLI, R. 1948 — An index for establishing the degree of maturity in plant communities. *J. Ecol.* 36: 85—90.

SHIMADA, Y. 1961 — An analytical study on the successional change of the *Miscanthus* type vegetation in native grassland owing to cattle and sheep grazing. *Rep. Stud. Upland Farm. Kawatabi Farm*, Tohoku Univ. 1957—1960, 57—63.

SUGANUMA, T. 1966 — Phytosociological studies on the semi-natural grasslands used for grazing in Japan, I. Classification of grazing land. *Jap. J. Bot.* 19, 2: 255—276.

SUGANUMA, T. 1967 — Phytosociological studies on the semi-natural grassland used for grazing in Japan, II. Ecological strata in pasture vegetation. *Bot. Mag. Tokyo*, 80, 946: 145—160.

SUZUKI, T. & ABE, Y. 1959 — La recherche des groupements végétaux aux prairies et aux pâturages au Japon dans la région d'Aso et de Kuzyu. *Jap. J. Ecol.* 9, 2: 75—79. (Jap./French).

SUZUKI, T. 1966 — The highest vegetation units of Japan and their areas. *Pedologist* 10, 2: 1—7. (Jap./Eng.).

YOSHIDA, S. 1950 — The relation between difference of cutting time and the plant succession of Sasa-land. *Bull. Inst. Agr. Res.*, Tohoku Univ. 2: 187—218. (Jap./Eng.).

YOSHIDA, S. 1950 — A study on the grassland types and the plant succession of Bokuya in Japan. *Ibid.* 2: 347—367. (Jap./Eng.).

YOSHIDA, S. 1956 — Ecological studies on Bokuya in Japan. *Ibid.* 7: 191—207. (Jap./Eng.).

YOSHIOKA, K. 1958 — Ecological studies on Japanese pine forests, Tokyo. (Jap.).