

## Secondary Succession of Herbaceous Communities in Japan : a Case Study in Sugadaira, Central Japan\*

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### Synopsis

Changes of floristic composition were observed for 7 years in an experimental field of secondary succession. In the 1-year-old stand, *Echinochloa crus-galli* var. *crus-galli* was the dominant species, and *Chenopodium album* and *Digitaria violascens* were important constituents. The sequence of dominant species during the succession was *Erigeron* spp. (*Erigeron annuus*, and *E. canadensis*) in 2-year-old stands, and *Artemisia princeps* in 3-year-old stands. *A. princeps* maintained its dominance from 4-year-old to 7-year-old stands. *Miscanthus sinensis* was established in the 3-year-old stands and increased in later stages. *Rumex acetosella* and *Oenothera parviflora* were important constituent species during succession. Four stages of secondary succession were recognized in herbaceous stages by different life-forms: summer annual, biennial (winter annual), perennial herb and perennial grass. Comparing secondary succession in various sites in temperate regions, the dominant species of each stage was similar in their life form. Raunkiaer's life-form spectra change from the therophyte type in the 1- and 2-year-old stands to hemicryptophytes and chamaephytes in later stages of succession. The dominant disseminule form in the 1-year-old stand was clitochore, and anemochore increased in the later three stages. The type of life history of the dominants was the same in the same seral stage among the sites in temperate regions.

Key words ; Secondary succession, Experiment, Mechanism

### Introduction

This paper describes the results of a 7-years experiment on secondary succession in a herbaceous stage in Sugadaira, Central Japan. In order to collect quantitative and precise information on succession, I recorded the change of species composition on a single stand experimentally prepared. In this paper, changes in the floristic composition, life-form spectra and disseminule-form spectra of seral stands are reported.

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A series of experimental studies of secondary succession in the herbaceous stage in Japan had been commenced by NUMATA and YAMAI (1955) and NUMATA (1956, 1982), NUMATA and SUZUKI (1958). In U.S.A., OOSTING (1942), KEEVER (1950), BARD (1952), QUARTERMANN (1957), BAZZAZ (1968), and DANIEL and PLATT (1968) have observed the succession on abandoned fields. In Central Bohemia, Czechoslovakia, OSBORNOVA et al. (1990) described the secondary succession in old fields. Recently, experimental studies of secondary succession have been carried out by SCHMIDT (1981) in Göttingen, BORNKAMM and HENNIG (1982) in Berlin and ITO et al. (1990) in Japan.

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Taxonomic nomenclature follows J. OHWI (1972).

### Study site and Method

Sugadaira is situated at 36° 30' N lat., 138° 27' E long., and 1,300 m altitude. The climate of Sugadaira is cool temperate, the mean annual temperature and precipitation being 6.5 C and 1,225 mm respectively. The soil is an andosol originating from volcanic ash.

The experimental plot of 29m×15m was set up on the campus of Sugadaira Montane Research Center, University of Tsukuba, where it had been used as a tree nursery.

The plot was divided into 5 subplots of 5m×15m, whose vegetation was cleared one by one for 5 years from 1975 to 1979 and allowed to recover under natural condition.

In each subplot, 10 steel quadrats of 1m×1m were laid out at points regularly spaced at 2 m along to parallel lines 2 m apart. In the subplot prepared in 1975 (1975 plot), 9 quadrats were laid out in one half of the plot, and the other half was kept bare through the experimental period for control. Because the observations were continued for 7 years on 5 subplots in successive year, five replicate measurements were possible for 1-year-old, 2-year-old and 3-year-old stands. 4, 3, 2 and 1 replications were made for 4-year-old, 5-year-old, 6-year-old and 7-year-old stands, respectively. In this context, 7-year-old stand means the stand elapse 7 years after clearance. The importance value of the species was expressed as an average of these replications.

The ground was cleared by eliminating all parts of plant including roots and rhizomes, except buried seeds, using a rake after plowing by a cultivator in April of the experimental years (Fig. 1). In the present paper, the plot prepared as described above is defined as the initial stand of secondary succession.

The soil properties of the plot prepared in 1975 were 30 % in loss of ignition, 0.17 % in the nitrogen content and 5.5 in pH value.

The total number of buried seeds was 21,389 in one square meter of soil to a depth of 5 cm, including seeds of *Portulaca oleracea*, *Echinochloa crus-galli* var. *crus galli* and *Elsholtzia ciliata* (TAKAHASHI and HAYASHI 1978).

Plant community investigations were carried out at approximately 1-month intervals for

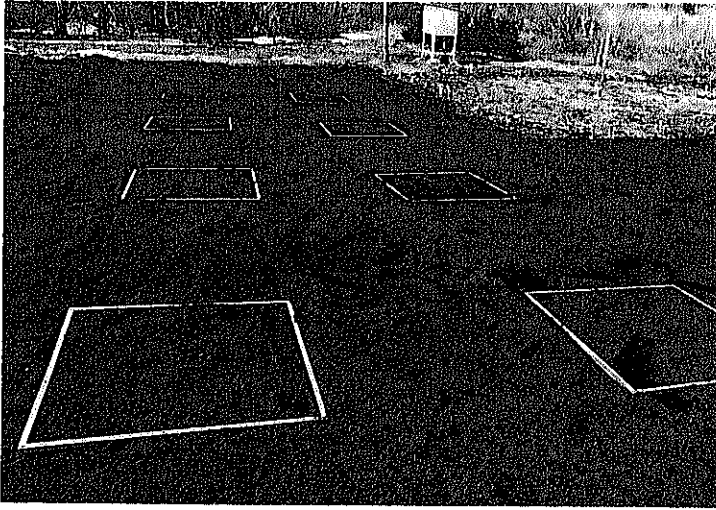


Fig. 1. The initial stand of secondary succession, which was prepared by eliminating all plant parts except soil buried seeds.

each subplot. The maximum plant height and cover were measured for each constituent species in the quadrats, and occurrence frequency in 10 quadrats was counted (9 quadrats in 1975 plot). Using these three biological measures, I calculated Numata's summed dominance ratio (SDR), which is a kind of importance value (NUMATA 1979).

The equation is as follows :

$$\text{SDR} = (\text{H}' + \text{C}' + \text{F}') / 3$$

where, H', C' and F' are relative height, relative cover and relative frequency.

### Results

The change of floristic composition from the 1-year-old stand to the 7-year-old stand is given in Table 1. Fifty-nine species were found in the successional stands throughout the experimental period. The species occurring in all stands from year 1 to year 7 in age were 9 in number including *Artemisia princeps*, *Oenothera parviflora* and *Rumex acetosella*. The dominant species of the 1-year-old stand was *Echinochloa crus-galli* var. *crus-galli*. *Digitaria violascens*, *Polygonum persicaria* *Rumex acetosella* and *Chenopodium album* were important constituents of the initial stand.

The 2-year-old stand was dominated by *Erigeron annuus*, *Erigeron strigosus* and *E. canadensis* which are biennials (winter annuals). In the 3-year-old stand, *Rumex acetosella*, *Artemisia princeps* and *Erigeron annuus* were dominants in similar importance value. From 4-year-old to the 7-year-old stand, *Artemisia princeps* maintained its dominance. In the 5-year-old stand the importance value of *Miscanthus sinensis* increased gradually, but

Table 1. Species composition of the seral stages in secondary succession at the experimental field

Species	Years after abandonment	Importance value (SDR)						
		1yr	2yr	3yr	4yr	5yr	6yr	7yr
<i>Artemisia princeps</i>		11.3	34.6	55.2	92.2	78.1	95.1	100.0
<i>Oenothera parviflora</i>		22.2	39.2	35.5	45.0	48.1	63.5	68.4
<i>Rumex acetosella</i>		51.4	80.9	84.2	50.7	52.6	46.3	45.7
<i>Oe. parviflora</i> (rosette)		23.7	15.5	25.8	46.6	48.1	47.5	40.1
<i>Erigeron annuus</i> (rosette)		18.6	12.4	15.9	12.4	27.3	22.3	34.9
<i>Cabystegia japonica</i>		20.3	18.7	34.9	27.3	34.4	27.6	26.4
<i>Hierochloe odorata</i>		2.1	6.7	7.9	22.5	4.2	37.9	25.1
<i>Picris hieracioides</i> var. <i>japonica</i>		2.2	2.8	2.3	5.3	6.0	5.0	3.0
<i>Stellaria media</i>		12.5	4.3	1.3	0.4	0.6	2.7	1.9
<i>Cerastium holosteoides</i> var. <i>hallaisanense</i>		8.1	2.9	13.5	7.8	3.0	1.0	1.9
<i>Echinochloa crus-galli</i> var. <i>crus-galli</i>		72.5	6.6	•	1.0	•	•	•
<i>Polygonum persicaria</i>		51.6	•	•	•	•	•	•
<i>Chenopodium album</i>		35.4	•	•	•	•	•	•
<i>Portulaca oleracea</i>		26.8	•	•	•	•	•	•
<i>Capsella bursa-pastoris</i>		1.8	•	•	•	•	•	•
<i>Polygonum lapathifolium</i>		0.5	•	•	•	•	•	•
<i>Rorippa indica</i>		18.5	4.3	•	•	•	•	•
<i>Digitaria adscendens</i>		6.6	0.3	•	•	•	•	•
<i>Panicum bisulcatum</i>		6.0	0.7	•	•	•	•	•
<i>Elsholtzia ciliata</i>		40.9	5.2	3.2	•	•	•	•
<i>Commelina communis</i>		44.8	2.5	5.5	•	•	•	•
<i>Erigeron annuus</i> (seedling)		5.4	0.8	0.3	•	•	•	•
<i>Erigeron canadensis</i> (rosette)		8.3	0.2	0.8	•	•	•	•
<i>Digitaria violascens</i>		64.2	12.9	1.1	0.5	•	•	•
<i>Erigeron canadensis</i>		•	40.1	15.9	1.8	1.0	4.0	•
<i>Dactylis glomerata</i>		•	2.9	2.2	3.6	2.8	1.3	•
<i>Agrostis clavata</i>		•	1.6	0.9	1.9	2.1	5.6	•
<i>Trifolium repens</i>		•	1.5	0.1	1.2	5.9	2.6	•
<i>Erigeron</i> spp.*		•	65.0	28.6	13.8	5.4	15.7	16.9
<i>Miscanthus sinensis</i>		•	3.6	8.0	7.9	25.3	19.4	29.7
<i>Lysimachia japonica</i>		•	0.4	1.2	1.2	0.6	1.7	5.5
<i>Hypericum erectum</i>		•	0.5	2.2	3.2	3.6	5.8	2.9
<i>Salix integra</i>		•	4.8	7.6	22.2	24.5	39.6	7.5
<i>Picris hieracioides</i> var. <i>japonica</i> (rosette)		•	0.6	•	•	2.1	3.7	11.4
<i>Geranium thunbergii</i>		•	•	4.9	11.1	28.8	35.0	33.7

Table 1. . continued

Species	Years after abandonment	Importance value (SDR)						
		1yr	2yr	3yr	4yr	5yr	6yr	7yr
<i>Larix leptolepis</i>		•	•	0.7	1.7	10.1	2.3	8.9
<i>Salix sachalinensis</i>		•	•	5.4	4.2	7.8	8.5	4.2
<i>Eupatorium lindleyanum</i>		•	•	1.4	4.4	1.1	1.8	3.3
<i>Artemisia montana</i>		•	•	•	1.5	1.3	2.7	•
<i>Agrimonia pilosa</i>		•	•	•	•	0.6	1.3	2.8
<i>Betula platyphylla</i>		•	•	•	•	5.6	9.1	1.9
<i>Poa pratensis</i>		•	•	•	•	0.3	1.5	•
<i>Agrostis alba</i>		•	•	•	•	•	1.0	8.1
<i>Lysimachia clethroides</i>		•	0.3	0.6	•	2.0	•	•
<i>Veronica arvensis</i>		•	0.2	0.3	•	•	•	•
<i>Lotus corniculatus</i>		0.3	•	•	•	2.0	•	•
<i>Petasites japonicus</i>		0.8	•	2.2	•	1.8	•	•
<i>Lespedeza bicolor</i>		1.3	•	•	9.1	•	•	•
<i>Salix bakko</i>		0.6	•	•	1.7	•	•	•
<i>Moehringia lateriflora</i>		•	0.3	•	•	•	2.8	•
<i>Muhlenbergia japonica</i>		•	0.9	•	0.5	•	•	•
<i>Carex nervata</i>		•	0.3	•	•	•	1.8	•
<i>Taraxacum officinale</i>		•	•	•	0.4	•	•	•
<i>Phleum pratense</i>		•	•	•	•	2.0	•	•
<i>Festuca ovina</i>		•	•	•	•	2.3	•	•
<i>Spiranthes sinensis</i>		•	•	•	•	2.1	•	•
<i>Pinus densiflora</i>		•	•	•	•	4.0	•	•
<i>Seseli ugoensis</i>		•	•	•	•	1.9	•	•
<i>Malus sieboldii</i>		•	•	•	•	2.0	•	•
<i>Populus sieboldii</i>		•	•	•	•	1.9	•	•
<i>Toisusu urbaniana</i>		•	•	•	•	•	2.7	•
<i>Rubus parvifolius</i>		•	•	•	•	•	•	3.8
		25	29	27	26	34	28	21

\**Erigeron* spp. include *Erigeron annuus*, *E. strigosus* and *E. pseudoannuus*

subsequent growth was delayed due to grazing of belowground parts of plants by voles during the winter. If the voles had not grazed the rhizomes and roots, *M. sinensis* might have increased considerably up to the 7-year-old stand. *Rumex acetosella* and *Oenothera parviflora* were important members in all stands during the succession. The 2-year-old stand denuded in 1977 was dominated by *Oenothera parviflora* instead of *Erigeron annuus*. *Stellaria media* and *Cerastium holosteoides* var. *hallaisanense* were constituent species in all stands though they had small importance values. It was noticeable that the trees and shrubs such as *Salix* spp., *Pinus densiflora*, *Betula platyphylla* and *Larix leptolepis* occurred even at an early stage

of secondary succession. The 7-year-old stand prepared in 1976 was dominated by *Salix* spp.

Fig. 2A shows the monthly changes in SDR for the dominant species of each seral stage. Just after denudation in April, the stand was dominated by *Stellaria media*, immediately replaced by *Echinochloa crus-galli* var. *crus-galli*. The dominance of *E. crus-galli* var. *crus-galli*, however, was restricted to the 1-year-old stand. An alternation of dominant species was observed year by year in a sequence of *Erigeron* spp. in the 2-year-old stand and *Artemisia princeps* in the 3-year-old stand which did already occur in the initial stand. *Miscanthus sinensis* was established in the 3-year-old stand and grew gradually. After grazing by voles in the 3-year-old stand, *M. sinensis* recovered vigorously, but in the 6-year-old stand its

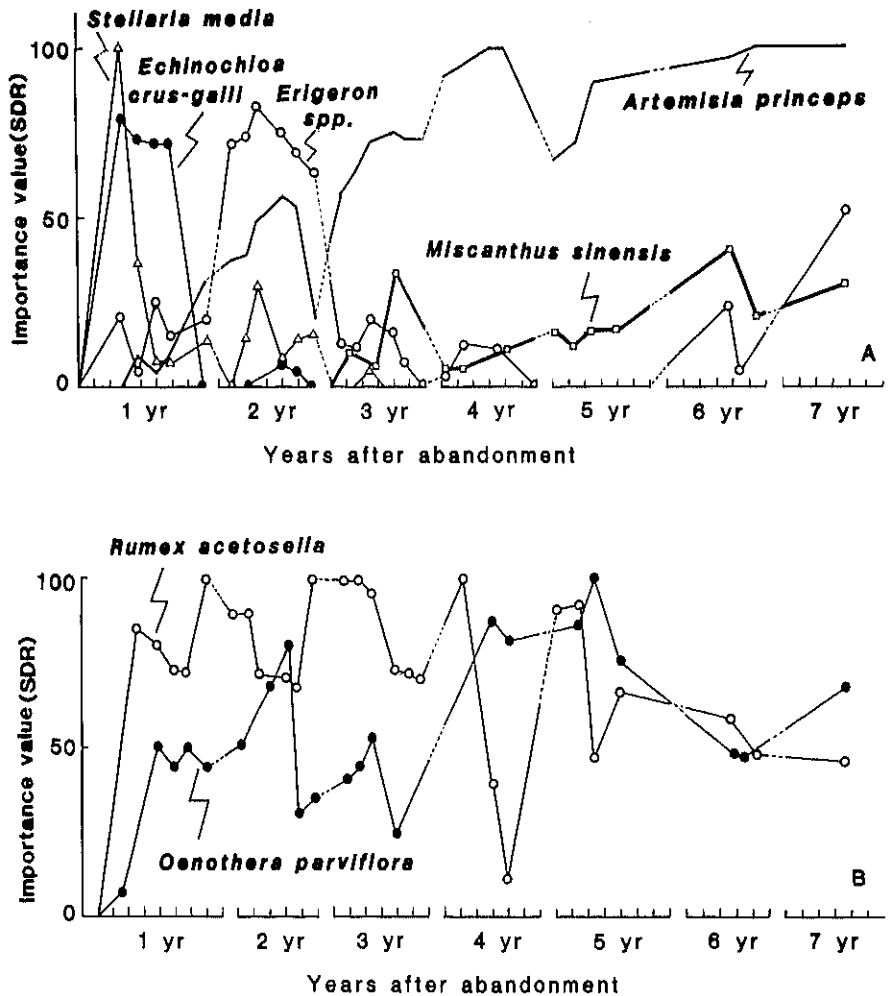


Fig. 2. Changes of importance value (SDR) of dominant species (A) and important constituent species (B) in the seral stands.

rhizome were grazed again. According to KANAMORI and TANAKA (1968), the vole may be *Microtus montebelli* (Hatanezumi). This is a case that mammals made plant succession delay by grazing the belowground parts of *M. sinensis*.

*Erigeron strigosus* increased from the 6-year-old stand and persisted as a constituent of the *M. sinensis* community in Sugadaira. Fig. 2B shows the monthly changes of SDR of *Rumex acetosella* and *Oenothera parviflora*, both of which decreased from 6 to 7-year-old stands.

Fig. 3 shows the change of life-form spectra of seral stands. Summer therophyte and winter therophyte were dominant life forms in the 1-year-old and 2-year-old stands. In the later stage of succession, hemicryptophytes became the dominant and geophytes and nanophanerophytes slightly increased. Fig. 4 shows the change of disseminule-form spectra from the 1-year-old stand to the 7-year-old stand. In the 1-year-old stand, the clitochore type ( $D_4$ ) was dominant. The anemochore type ( $D_1$ ) increased from the 2-year-old stand and dominated after the 3-year-old stand. The bolochore type ( $D_3$ ) increased during the succession though the importance value was small.

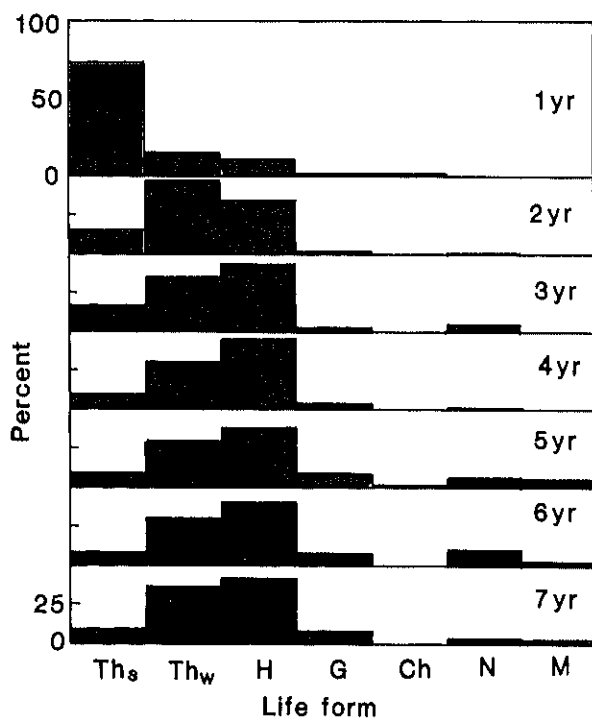


Fig. 3. Changes of life-form spectra from the 1-year-old stand to the 7-year-old stand.

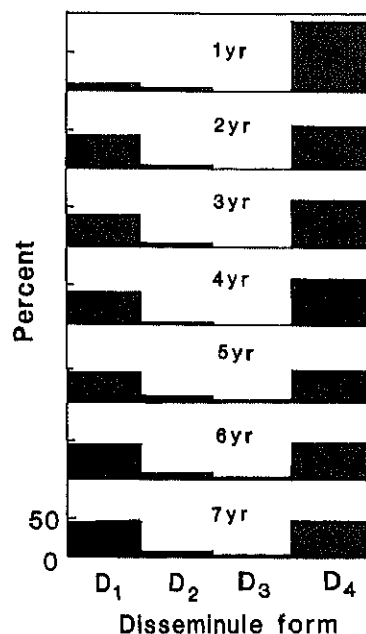


Fig. 4. Changes of Numata's disseminule form spectra from the 1-year-old stand to the 7-year-old stand.  $D_1$ : anemochore,  $D_2$ : zoochore,  $D_3$ : bolochore,  $D_4$ : clitochore.

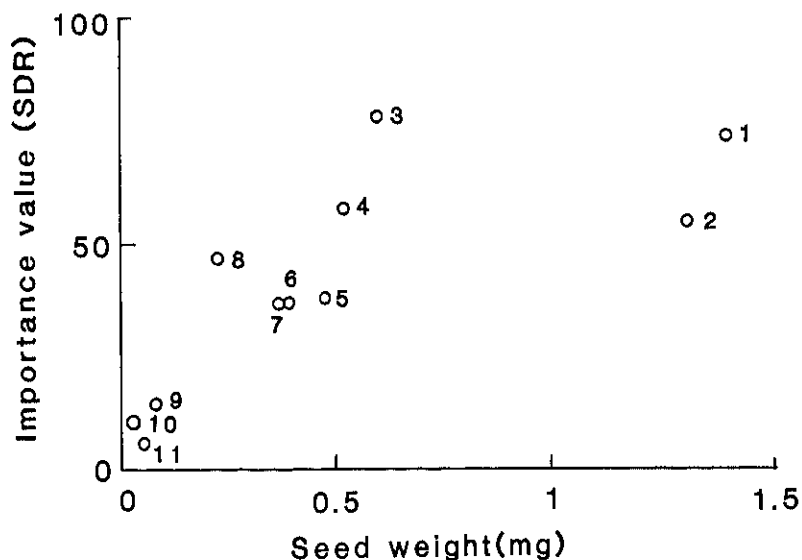


Fig. 5. Relationship between seed weight and importance value (SDR) of constituent species in the 1-year-old stand.

1. *Echinochloa crus-galli* var. *crus-galli*, 2. *Polygonum persicaria*, 3. *Rumex acetosella*, 4. *Chenopodium album*, 5. *Oenothera parviflora*, 6. *Digitaria violascens*, 7. *Stellaria media*, 8. *Elsholtzia ciliata*, 9. *Portulaca oleacea*, 10. *Erigeron annuus*, 11. *Artemisia princeps*

The relationship between SDR and seed weight of the species is shown in Fig. 5. It is clear that in the 1-year-old stand, the species with heavier seeds were larger in importance value. This suggests that the species having heavy seeds are advantageous at the initial stands of secondary succession by producing a larger seedlings.

### Discussion and Conclusion

In this experiment, the important constituent species of the 1-year-old stand were summer annuals such as *Echinochloa crus-galli* var. *crus-galli*, *Digitaria violascens*, *Chenopodium album* and *Polygonum persicaria*. Any species among these, however, may dominate in a 1-year-old stand according to varying initial conditions such as soil fertility, way of denudation, season and seral stages cleared. For example, in the stands with fertile soil such as abandoned crop lands, *Chenopodium album* and *Digitaria adscendens* may be expected to be dominants (Kuwabara 1957, Hayashi 1967, 1969, 1977). In the lowland regions of Japan, *Ambrosia artemisiifolia*, *Digitaria adscendens* and *Setaria viridis* were dominants in 1-year-old



stands (NUMATA 1956, HAYASHI 1977, MATSUMURA et al. 1988, ITO et al. 1990). If the initial stand is prepared in autumn or in early spring, these stands would be dominated by winter annuals such as *Bromus catharticus*, *Stellaria media* and *Capsella bursa-pastoris*. In fact, *Stellaria media* predominated in the stand in Sugadaira just after denudation in April. An initial stand of primary succession, such as succession on lava flow and on volcanic ash, was dominated by *Miscanthus sinensis*, *Polygonum cuspidatum*, *P. sachalinense* and *Petasites japonica* (TEZUKA 1961, TAGAWA 1964, ITO and HARUKI 1984).

The dominants in pioneer stage of secondary succession were similar in various sites of the world. For example, *Chenopodium album* and *Digitaria sanguinalis* (*D. adscendens*) are common dominant species in the pioneer stage of Korea (CHANG and YUN 1960), Germany (SCHMIDT 1981), U.S.A. (OOSTING 1942, KEEVER 1950) and Japan. *Ambrosia artemisiifolia* is the common dominant in the initial stands of U.S.A. and Japan (DANIEL and PLATT 1968, BARD 1952, BAZZAZ 1968, ITO et al. 1990). *Erigeron* spp. (*Erigeron annuus*, *E. canadensis*, *E. sumatrensis*) are common dominants in the biennial (winter annual) stages in Korea, U.S.A., Germany and Japan. In the perennial herb stage, the dominant species are *Artemisia* spp. in Korea, Japan and Czechoslovakia (OSVORNOVA et al. 1990), *Solidago* spp. in U.S.A., Germany (BORNKAMM 1984) and Japan HAYASHI (1977). *Eupatorium chinense* var. *sachalinense* and *Crassocephalum crepidioides* were seen in the stands after clearing forests. *Eupatorium* spp. are a successional dominant in perennial herb stage in Southeast Asia (KOCHUMEN 1966, KUSHWARA et al. 1981, TSUCHIDA 1983). According to OOSTING (1942), KEEVER (1950) and QUARTERMANN (1957), *Aster pilosus* often predominate in the perennial herb stage in U.S.A.. The perennial grass stage is dominated by *Miscanthus sinensis* in Japan and Korea, *Andropogon* spp. in U.S.A., and *Poa* spp. and *Calamagrostis* spp. in Germany. VARTIAINEN (1980) reported that *Calamagrostis stricta* and *Festuca rubra* predominated in the land lift area in Finland (64° 12'-65° 46' N and 23° 33'-25°-12' E) at the second stage of succession. *Calamagrostis* spp. are the dominants of the grasslands of subalpine zone of Central Japan and Northern Hokkaido (TSUCHIDA 1982). OKA (1984) reported that *Leersia hexandra* was a dominant in a stage following herbaceous dicotyledonous stage of secondary succession in paddy fields of Taiwan.

According to MARUYAMA et al. (1984a, b), a cut slop of the road in forest was dominated by *Miscanthus sinensis*, *Eupatorium chinense* var. *simplicifolium* and shrub of *Weigela hortensis*. In this case, the dominant pioneer species were perennial grasses which are seen as dominants in the pioneer stage of primary succession in Japan. KAMEGAWA (1971), who investigated a succession of the roadside of the Tomei Highway running through the warm temperate region in Japan, described a sequence of dominant species of *Erigeron canadensis*, *Artemisia princeps* and *Miscanthus sinensis*. This sequence is similar to the results of present experiment.

Based on these results, one may conclude that four stages are recognized by dominants of different life-forms during herbaceous stages in secondary succession. The life-forms in corresponding stages are the same for different sites of the world, though the dominant

species are different from site to site. A common ecological characteristic of dominant species in 1-year-old stands in various sites is to produce heavy clitochore seeds, which remain dormant, buried in the soil. In general, heavier seeds produce larger seedlings, which can survive under severe condition on bare soil. That is one of the reason the rank of constituent species of communities in a 1-year-old stand is closely correlated with seed weight (TAKAHASHI and HAYASHI 1977). The dominant species in subsequent stages may be similar also in the type of life history: *Erigeron* spp. in second stage, and *Artemisia princeps*, *Solidago* spp. and *Aster* spp. in third stage, and *Miscanthus sinensis*, *Andropogon* spp. and *Poa* spp. in fourth stage (HAYASHI 1979, 1984a, b) These species are seemed to be successional equivalents in secondary succession.

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