Facts, Causal Analyses, and Theoretical Considerations on Plant Succession

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Introduction

Although plant succession is one of the most important problems in ecology, the accumulation of data on it is not very large. Japan is a relatively small archipelago, and it is difficult to find concrete examples of succession even in more remote parts of the most northerly island of Hokkaido or in the southern island of Kyushu. Even those descriptive examples that do exist are few. Until recently, the causal analysis of succession has been inadequate. There are explanations of the concepts of primary and secondary succession, the replacement of seral stages by sun and shade trees, succession and climax, the difference in climaxes corresponding to climatic regions, etc. in high school biology textbooks; however, there are very few causal analyses.

Migration and ecesis of plants were pointed out by A. von Humboldt (1806), but Kerner (1863) was the pioneer of the concrete studies of successional relationships among various vegetation types in the Danube basin. An American writer, Thoreau (1860) observed cyclic succession and discussed nature conservation based on the successional view. After that, Cowles (1899) wrote a monumental work on the succession of sand dunes along the coast of Lake Michigan, and Clements (1905) stated the concept, kinds, causes and general rules of plant succession followed by his epoch-making monograph (Clements 1916).

I. Various Problems in Plant Succession

1. Characteristics of Pioneer Herbs and Grasses

Summer annuals and then winter annuals appear in secondary succession as pioneers. Many light propagules are produced by pioneers in open habitats, and a few heavy propagules are produced by tree species in shade habitats(Salisbury 1942). However, there is one exception, that of first year pioneers such as *Ambrosia artemisiaefolia* var. *elatior* on a denuded quadrat having rather heavy propagules: 400mg/100 grains (Hayashi and Numata 1967). Propagules of this first year pioneer germinate between March and June, and many of them germinate earlier and almost simultaneously. The after-ripening period is long (Table 1), and low and/or variable temperatures in the winter promote germination in the spring. The temperature of germination is rather low, and the light requirement is not compulsory. These are characteristics of the first year pioneer species.

In contrast to this, the second year pioneer species have light, widely dis-

Table 1. Germination rate of species according to after-ripening age and incubation temperature (Hayashi and Numata 1967)

Weeks after harvesting	0	7			11			17			27		
Temperature of incubation (°C)	20	10	20	30	10	20	30	10	20	30	10	20	30
Ambrosia artemisiaefolia var. *elatior*	0	0	0	0	0	1	18	0	2	28	0	14	27
Setaria lutescens	0	0	0	0	0	0	0	0	0	0	38	49	1
S. viridis	0	0	0	0	0	0	0	0	0	0	0	0	0
Erigeron annuus	86	0	90	58	0	86	73	0	51	90	0	80	79
E. sumatrensis	94	62	78	75	34	67	62	89	90	75	80	84	75
Oenothera muricata	46	0	82	85	0	93	88	0	88	87	0	63	83
Chenopodium album var. *centrorubrum*	15	5	47	24	32	57	40	28	64	38	27	52	25

Table 2. Germination rate of pioneer or similar species under controlled temperatures (22° and 30°) and light intensity (2,000 lux) after storage under various conditions.

Storage condition Species Weeks*	Under room condition			0°—3° stratification		
	7	14	27	4	8	20
Ambrosia artemisiaefolia var. *elatior*	0	18	27	8	50	96
Setaria lutescens	0	0	0	0	0	46
Erigeron annuus	58	73	79	73	64	73
E. sumatrensis	75	62	75	82	74	58
Oenethera muricata	85	88	83	67	82	85
Chenopodium album var. *centrorubrum*	24	40	25	27	45	18
Amaranthus retroflexus	32	86	97	2	22	3

* Number of weeks stored under various conditions.
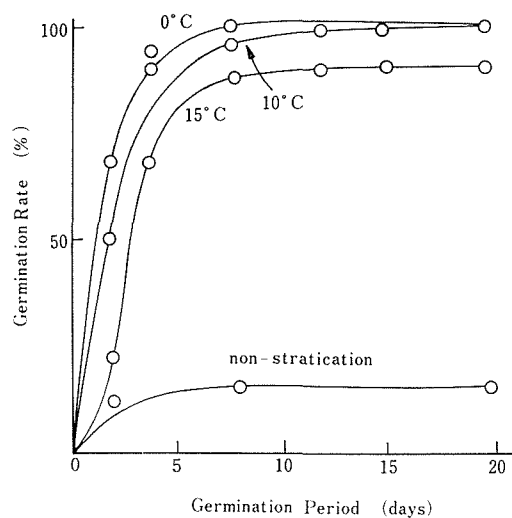
Fig. 1. 1. Differences of the germination behavior of *Ambrosia* seeds according to temperatures during stratification of 60 days. The after-ripening age at the time exposed to the low temperature is 85 days.
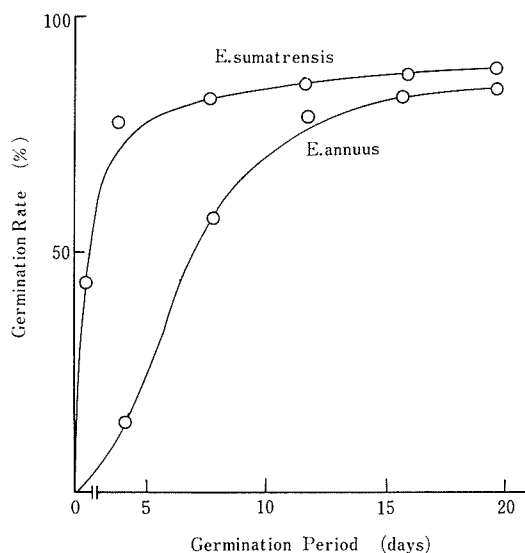
Fig. 1. 2. The germination behavior of *Erigeron annuus*
and *E. sumatrensis* without stratification.

persive propagules, such as *Erigeron* spp. 3mg, *Capsella bursa-pastoris* 6mg, *Amaranthus viridis* 24mg, *Digitaria adscendens* 30mg, *Oenothera muricata* 45 mg, and *Chenopodium album* 47mg per 100 grains. These are 1/10 to 1/100 times as light as the propagules of *Ambrosia*, showing high rates of germination (Table 2) and no effect of vernalization (Fig. 1). They survive the winter with small rosettes. The first and second year pioneer plants have ecological differences in the mode of life as mentioned above; however, both of them have a remarkable similarity ecologically to naturalized plants. According to an example in New Jersey in the U. S. A., pioneer stages of secondary succession in old fields were occupied by many non-indigenous plants (Bard 1952). A general rule of secondary succession, the replacement of dominant species from annuals to perennials, is recognized even in biotic succession on denuded rocks of the intertidal zone: from the pioneer stage of diatoms to the stage of sedentary biotic communities on rocks composed of barnacle, *Hizikia fusiforme*, green layer, etc. depending on vertical life zones under the influence of limpets (Odaka and Numata 1979).

2.   Characteristics of Pioneer Trees

Is either of two large life-form groups of plants, trees and herbs, an evolutionary new group ? One assumption is that trees are new life-forms and have extended their distribution adapting to the ecological conditions of the earth. Another is that trees are old, and afterward herbs and grasses without secondary growth appeared with short, creeping, etc. growth habit (Bancroft 1931). In general, herbs and grasses dominate in cold areas, and trees dominate in warm areas in the present geographical distribution, while the first seed plants seem to develop in the tropics. In the endemic flora of oceanic islands isolated from the continent, trees are dominant, and annual herbs and grasses are few. These facts may support an assumption that trees were constituents of the oldest vegetation (Numata 1971). However, trees in oceanic islands might be a secondary

specialization which does not necessarily mean old or primitive. Nevertheless, plants migrating on land from the sea in ancient times were herbaceous in a broad sense, and then arborescent forms appeared. However, when the evolution of phanerogams since the Tertiary is considered, it is evolution from arborescent Gymnospermae. In this case, herbaceous forms evolved from arborescent forms.

There are two types of growth rhythm in trees, and the ecological characteristics of pioneer trees are similar to those of pioneer herbs. Pioneer trees such as *Salix caprea*, *Populus tremula*, etc. grow quickly in the early stage, but their growing ability degenerates shortly thereafter. On the other hand, shade trees such as *Abies alba*, *Taxus baccata*, etc. grow slowly in the young stage, and their growing ability continues for long (Knapp 1954).

Budowski (1961) tabulated ecological characteristics of trees in seral stages of tropical humid forests. The number of species of pioneer trees is limited; however, the number of tree species increases as succession proceeds. Pioneer trees have wide areas of distribution, occupying homogeneous, dense, low storeys. Their early growth is rapid, having short longevity, small tolerance, slender and light wood; they have small and long-lived propagules dispersed by birds, bats, wind, etc., and do not regenerate in the shade. In the grassland vegetation of Japan, the percentage of phanerophytes is almost zero in *Zoysia japonica* pastures, 5 % in *Pleioblastus distichus* var. *nezasa–Z. japonica* pastures, 20 % in *P. variegatus* var. *nezasa–Miscanthus sinensis* and *M. sinensis* meadows, and 25 % in *Sasa* spp. meadows (Numata 1965). These trees gradually become dominant in the following stages.

3. The Replacement of Dominants

The replacement of dominants is the most remarkable phenomenon in succession the mechanism of which will be discussed later. The removal of dominants experiment in permanent quadrats was conducted (Numata 1956). The first year dominant, *Ambrosia artemisiaefolia* var. *elatior* was removed by cutting in June, and the second year dominant, *Erigeron annuus* dominated in August of the same year. The removal of a dominant or co-dominants, as a rule, promotes the progression of secondary succession in early stages. Similar experiments were conducted by Tanabe (1970) at another site, and similar results were obtained. However, temporary, apparent promotion of succession was limited for only two to three years in early stages.

4. Orthosere and Plagiosere

The process of vegetation development in a denuded permanent quadrat is progressive, orthoseral succession. Due to the difference in the composition of the buried-seed population in the soil, the dominants of pioneer stages are sometimes different, however similar orthoseres may be observed in geographically close areas.

The direction of orthoseres is sometimes distorted or stopped. *Miscanthus sinensis* tallgrass meadows in northeastern Japan change to *Zoysia japonica* shortgrass pastures for two or three years under the grazing stress of cattle. The *Z. japonica* pasture degenerates to bare ground under heavy grazing and trampling, and sometimes to weedy pastures with many non-palatable plants, such as *Pteridium aquilinum* and *Rhododendron kaempferi*.

Burning promotes the germination of hard seeds of the shrubby legume,

Lespedeza bicolor, and *Miscanthus sinensis* meadows change to *L. bicolor* shrublands (Iwata 1971). These biotic factors, grazing, trampling, burning, etc. are the cause of plagioseral succession.

   5. Characteristics of Climax Trees

   Compared with pioneer species, climax tree species are limited in distribution, slow in growth, long in the life span and mostly tolerant. The dispersal of propagules is caused by gravity, mammals, rodents, birds, etc., with thick and hard wood, large and short-lived propagules, and so on (Budowski 1961).

   The Douglas fir (*Pseudotsuga menziesii*) is a pioneer tree in the vicinity of Seattle, western North America, however it becomes a climax tree in the northern dry areas (Franklin and Dyrness 1973). The lodgepole pine (*Pinus contorta*) is a pioneer tree in the lower part of the Cascade Mountain Range; however, it becomes a climax tree at higher altitudes. *Larix leptolepis* is usually considered a pioneer sun tree particularly on volcanic materials in Japan, and that species above the tree line of Mt. Fuji is also considered to belong to a pioneer stage due to the youth of the volcano. Non-volcanic mountains and geologically old, dead volcanoes in Japan usually have an alpine shrub zone of *Pinus pumila*. However, young volcanoes, such as Mt. Fuji and Mt. Asama, have an alpine shrub zone of *Larix leptolepis*. This being so, *L. leptolepis* could be considered a climax shrub of the alpine zone of young volcanoes (Numata 1971).

   6. Succession of Vegetation and Soil

   There are many studies on soil formation or changes in relation to plant succession. Calcareous rocks of central Alps become alpine humus soil through rendzina soil by the accumulation of acid humus, and podzolization (Braun-Blanquet and Jenny 1926). Soils of abandoned fields accumulate organic material, increase the water-holding capacity and decrease the volume weight corresponding to the vegetation change from the pioneer stage to the oak-hickory climax through the pine stage (Billings 1938).

   The depth of the surface soil and total amount of nitrogen, etc. corresponded to the primary succession on volcanic material on the Island of Izu-Oshima (Tezuka 1961). The total amount of nitrogen was traced in the surface soil from the pioneer stage on bare ground to the *Pinus thunbergii* stage (Ohga and Numata 1965). The same thing is observed in agro-ecosystems as in the relationship between natural vegetation and natural soil. In the newly cultivated soil, particularly the volcanic ash soil in Japan, bases are lacking, and the soil reaction is strongly acidic. It has a large amount of organic material in surface soils such as forest soils, the ratio SiO_2/Al_2O_3 is small (i. e. the alminium of soil colloid being easily activated), nitrogen is supplied sufficiently, but phosphorus is not supplied much due to the fact that phosphorus-absorbing power is strong in the volcanic ash soil. This newly cultivated soil becomes mature farmland soil over many years, and species and varieties of crops and weeds grow reflecting the soil change in the long-term succession of agro-ecosystems.

   7. Degree of Succession

   To measure the progression of succession quantitatively, the degree of succession was defined as follows (Numata 1961).

   $$DS = [(\textstyle\sum d \cdot l)/n] \cdot v$$

where d is the summed dominance ratio (SDR, 0~100), l is the life span (Th: 1, H, Ch, G: 10, N: 50 and M, MM: 100 depending on life-forms), n is the number of species, and v is the ground cover (100%=1). Using this DS, various grassland types were ordinated in the form of a DS-frequency curve (Numata 1969 —Fig. 2). To judge the grassland condition on the basis of such a successional diagnosis, the index of grassland condition (IGC) was proposed as follows (Numata 1962).
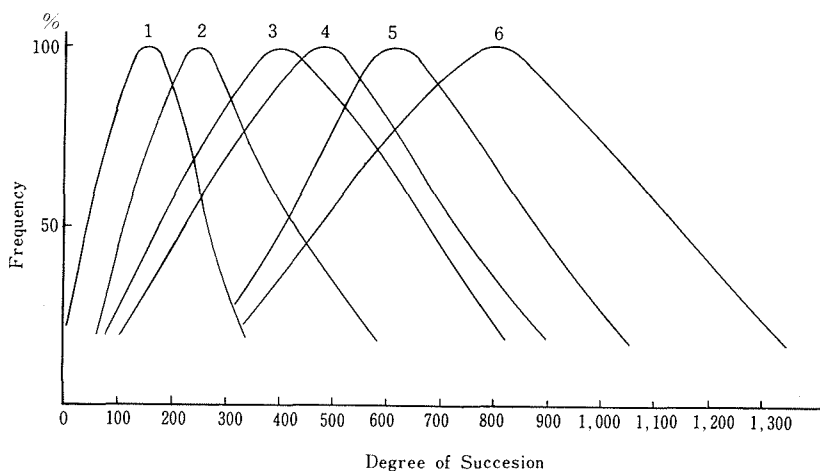

Fig. 2. The frequency curve of DS of grassland vegetation, i. e. the ordination of grassland types or stages by DS. **1**: *Erigeron* stage, **2**: *Zoysia japonica* stage, **3**: *Pteridium aquilinum* stage, **4**: *Miscanthus sinensis* stage, **5**: *Pleioblastus* stage, **6**: *Sasa* stage.

$$IGC = [(\sum d \cdot l \cdot g)/n] \cdot v$$

where g is the grazing rate (0~10) related to palatability.

These DS and IGC were devised mostly for grassland vegetation. To enlarge this idea to forest vegetation, the climax adaptation number (Curtis and McIntosh 1951) was added to the former formula as follows,

$$DS = [(\sum d \cdot l \cdot c)/n] \cdot v$$

where c (the climax adaptation number) is 1 for the pioneer species and 5 for the climax species (Numata 1971). An application of this formula is shown in Table 3. When two formulae of DS were compared, those indicate the same trend though DS including c is, nevertheless greater than DS without c (Sakura and Numata 1976). DS was applied to the spatial analysis of plant communities in the form of the isopleth of DS (Fig. 3, Numata et al. 1971). Homogeneity has been discussed from the viewpoint of the distribution pattern of individuals and species, and the coefficient of homogeneity for individuals and plant communities was proposed (Numata 1950). Structural analysis by the isopleth of DS may indicate one side of the community homogeneity and distribution pattern.

8. Distribution Pattern and Succession

In a review of the distribution pattern of plant communities, the viewpoint of dynamic ecology was introduced (Numata 1954). The studies of plant succes-

Table 3—1. The comparison of *DS* of vegetation including planted trees in
early stages of a young plantation of *Chamaecyparis obtusa*

Plot	Formula of *DS*		1 st year	2 nd year	3 rd year	4 th year	5 th year
A	{	(1)	718	548	596	646	502
		(2)	2,845	2,066	2,317	2,549	2,118
B	{	(1)	459	549	676	641	373
		(2)	1,715	2,029	2,561	2,423	1,446
C	{	(1)	340	704	888	763	367
		(2)	1,283	2,654	3,348	2,893	1,430

Table 3—2. The comparison of *DS* of vegetation except planted trees in
early stages of a young plantation of *Chameacyparis obtusa*

Plot	Formula of *DS*		1 st year	2 nd year	3 rd year	4 th year	5 th year
A	{	(1)	704	538	590	639	473
		(2)	2,783	2,018	2,284	2,516	1,975
B	{	(1)	443	526	647	604	319
		(2)	1,637	1,913	2,415	2,235	1,180
C	{	(1)	316	660	819	688	302
		(2)	1,162	2,436	3,000	2,516	1,104

(1) $DS = [(\Sigma\, dl)/n]\ v$

(2) $DS = [(\Sigma\, dlc)/n]\ v$
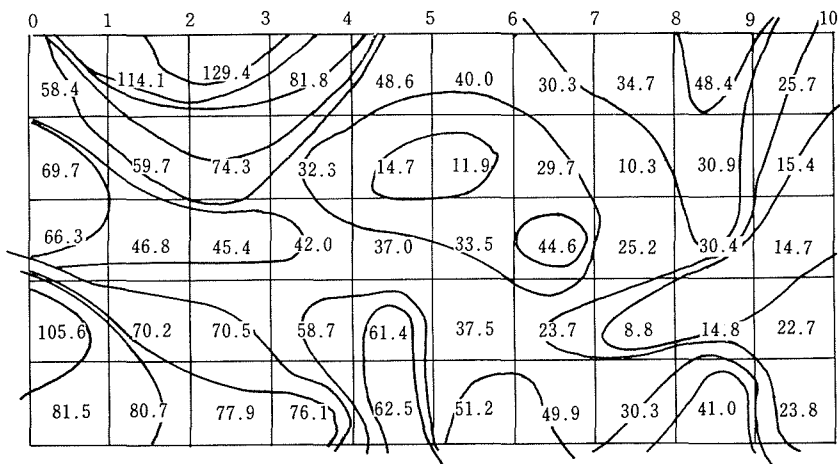
Fig. 3. The DS-isopleth of a weedy community in an
old-field (Numata, Ohga and Kaji 1971)

sion thereafter accompanied the statistical analysis of the distribution pattern, and
such a quantitative analysis is an important approach to plant succession (Numata
1959, Kershaw 1964). The species groups in the distribution pattern characteristic
of each seral stage were found in old-field succession (Whitford 1949), the sequence
of succession in bamboo forests (Numata 1955, 1965), and coastal vegetation
(Numata 1950) on the basis of the coefficient of homogeneity (Numata 1949,

Greig-Smith 1964). For such analyses, drawing of the dispersion map is very useful.

Farmland weeds are distributed contagiously at their emergence; however, the modes of distribution become random four weeks after the sowing of upland rice, and then they again become contagious (Niiyama and Numata 1969). The time when the distribution becomes random is the critical point allowable for the existence of weeds (Fig. 4). If the weeds are not removed beyond that critical
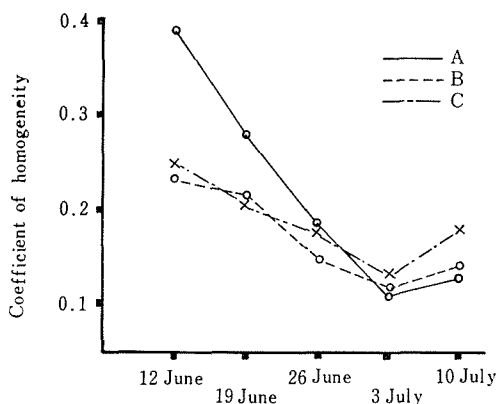

Fig. 4. Coefficient of homogeneity based on the cover (CH$_c$) in the treatment A, B, and C in the crop-weeds competition experiment. A, B and C are the sowing density treatments of upland rice: 5cm, 10cm and 15cm intervals. (Niiyama and Numata 1969).

point, the yield of upland rice will be remarkably reduced. This experiment suggested the allowable limit for growing weeds in farmlands. Even in man-made bamboo stands, thinning management to maintain a random distribution is the best method of producing good bamboo culms. The fact that the coefficient of homogeneity corresponded well with the relative importance of constituent species in a coastal grassland (Numata 1949) suggests the previously mentioned case in bamboo stands. A native bamboo stand as a topographical climax indicated a typical random distribution (Numata 1965).

9. Succession of Buried-seed Population

Succession is usually discussed on aboveground vegetation, however the buried-seed population is the actual forerunner of such vegetation. The underground succession, particularly that of the seed population, was traced from the pioneer to the climax stage in central Japan (Numata et al. 1964, Hayashi and Numata 1964, 1966, 1968, 1971). The floristic composition of aboveground vegetation and buried-seed population is not the same. The floristic composition of a buried-seed population includes some of the prior and later stages (Numata 1978). For example, the increase of perennial grasses (*Miscanthus sinensis*, etc.) and herbs (*Leguminosae*, etc.) of the following perennial grass stage was found in the soil of the pioneer *Erigeron annuus* stage. Each of the *Erigeron annuus*, *Imperata cylindrica* var. *koenigii*, and *Pinus thunbergii* stages has the buried seeds of constituent species of the former stages. When the aboveground vegetation is destro-

yed, the secondary succession from the pioneer stage will be repeated based on the buried-seed population, including the seeds of the pioneer species.

Considering the seed balance, the total number of buried-seeds per unit area at a time is called GSP (gross seed production), and the total number of seeds of a seral stage produced during one season per unit area is called SSP (seral seed production). To estimate the buried-seed population at an early stage of secondary succession, the total number of supplied seeds per unit area was estimated by the subtraction of the number of buried-seeds in June from that in December. The former is the rest of the buried-seeds after germination in the spring, and the latter is the sum total of buried-seeds newly added in the autumn. The apparent SSP of the *Ambrosia artemisiaefolia* var. *elatior* stage was 16,500 per 100 x 100 (area) x 1 (depth) cm³ soil. The apparent SSP includes seeds supplied from the outside.

The seed population dynamics of a plant community is shown by the formula: $s=(p+i)-(c+c'+o)$, where p is the production of seeds (SSP), i is the invasion of seeds into the community from outside. c and c′ are the consumption of seeds by germination and decay respectively. o is the loss of seeds from the community to the outside by various means of dispersal per unit area in one growing season. s is the storage of buried-seeds in the soil under a community per unit volume at a time. A fundamental equation of population growth is: $N_{t+1}=N_t+Births-Deaths+Immigration-Emigration$ (Harper and Whyte 1974). Here, $N_{t+1}-N_t=s$, Births=p, Deaths=c′, Immigration=i, and Emmigration=c+o (Numata 1978).

10. Succession and Production

As mentioned above, the author based his diagnosis of grassland conditions on the diagnosis of the degree of succession. In the *Miscanthus sinensis* grasslands surveyed all over the country (Numata 1966), SDR (the summed dominance ratio=the relative importance) of *M. sinensis* was 100 or nearly 100, SDR' (the relative SDR as the total of SDR of all species being 100) or *M. sinensis* was about 15, and the DS-frequency curves cover 100~1000 in DS the mode of which is 400~500. The similar type of distribution curves in the biomass–DS curve was forecasted and observed (Numata 1966) and was discussed in relation to the primary productivity of semi-natural grasslands in Japan (Numata 1970).

Thereafter, the biomass–DS relationship was enlarged to the vegetation unit–biomass–DS relationship (Okuda and Numata 1975, Tsuchida and Numata 1979). The grassland biomass in the above relationship was measured at the time of maximum biomass at the end of August or the beginning of September. The biomass is almost equal to the net production of the community in the current year. The biomass–DS curves were separated for different sociological or physiognomic units of grassland vegetations. This fact suggests the possibility of making a bridge between plant sociology and production ecology.

To compare the primary productivity of grasslands of different regions of the world, as was done in the IBP, the equality of dynamic status of grasslands is needed (Numata 1976). If the dynamic status of a grassland is different, the productivity is consequently different. Therefore, it is strongly proposed that DS should be checked for these comparisons.

11. Seral Niche

The term "niche" was originally used to indicate ecological situations in a food chain, however this has been enlarged at present to include such things as trophic, spatial and multidimensional or hypervolume niches (Odum 1971). Besides these, the author proposed the concept of seral niche or its equivalent (Numata 1969, 1971). One good example is found in the relationship between alien and indigeneous plants in the pioneer stages of secondary succession. Some species were dominants in their pioneer stages before the Meiji era (1867), but we cannot estimate exactly when. At present, the first year, the second year, or later dominants in the pioneer stages on bare grounds are almost completely occupied by aliens, such as *Ambrosia artemisiaefolia* var. *elatior*, *Erigeron annuus*, *Solidago altissima*, etc. Many of these have come from North America.

On the other hand, there are very few Japanese species that have been naturalized in North America. This fact seems to be due to ecological niches, which do not always mean spatial niches (Miyadi 1967), because the Japanese Islands were invaded by many alien plants, and North America was not. *Lonicera japonica* hangs its climbing stems from the canopy and trunks of planted forests in Pennsylvania, U. S. A. as shown to the author by Dr. J. McCormick in 1968. It is similar to *Pueraria lobata* in Japanese forests. *Lonicera japonica* is a ruderal plant climbing hedge of gardens or a component of the edge community of forests in Japan, and it is not similar to the noxious weed, *Pueraria lobata*. If *Lonicera japonica* in the U. S. A. is exactly the same species as the one in Japan, the difference in its ecology should be due to the difference of habitat.

Recently, the author was asked about the autecology of *Celastrus orbiculatus* by a U. S. botanist of the University of North Carolina. He says that that species has become a noxious weed there; however, it is not so in Japan. These examples show the different ecology of seral equivalents in different habitats.

The process of the naturalization of alien composite plants has not yet been clarified. However, the author observed the replacement of *Oenothera* species. The coastal vegetation on a sand-bar at Futtsu, Chiba Prefecture was measured in 1949, and a part of it was found to be the alien, *Zoysia macrostachya-Oenothera lamarckiana* community (Numata 1949). However, that *Oenothera* species was replaced thoroughly by *O. laciniata* (Mitsudera and Numata 1964). The replacement occurred in 1957 on the coast of Tokyo Bay and in 1960 on the Pacific Ocean side of Chiba Prefecture (Shinozaki 1973). This is a remarkable replacement of species belonging to the same seral niche. These replacements have occurred between indigenous plants and aliens and between former resident aliens and late comers.

II. Causal Analyses of Plant Succession

1. Light and Soil

An important factor in explaining the mechanism of plant succession has been the light factor. For example, the relative light intensity is 5~25% on the undergrowth in a forest and 1~3% on the ground surface under the shrub and/or herb layer. Saplings and young trees need a relative light intensity of more than 6.5% for sun trees and more than 5% for shade trees to grow in such a forest, and even then the light condition in forests is not sufficient in many cases.

However, if such trees emerge in a grassland, they have a chance to grow over the upper layer of vegetation, and such young trees continue to grow. The growth of young trees is better for shade trees in a forest, and the vegetation changes to a forest of shade trees over a long period (Oshima 1959). The importance of the light factor as the motive force of plant succession, such as in this case, has been noted by Boysen-Jensen (1932). There are many studies of analysing plant succession in relation to light conditions on the basis of primary production (Monsi and Oshima 1955, etc.)

There are many studies on the change of soil conditions accompanying the progression of plant succession. Some of them analysed soil formation by the reaction of plants and the replacement of associations with the newly formed soil conditions (Braun-Blanquet and Jenny 1926).

Such a chain of actions and reactions is considered as a motive force in plant succession. When the interaction occurs within a community, biome or ecosystem, it is recognized as an autogenic succession (Clements 1916). Following the Clements' idea, a biome as a social organism is born, grows, matures and dies due to inside causes, and such a life history of vegetation is plant succession.

Among the standards for judging climaxes, 1) physiographic change, 2) soil maturity, 3) mesophytism and 4) tolerance (Whittaker 1953) are related to environmental conditions. Among them, 4) is related to the light factor, and 1), 2) and 3) are related to the edaphic factor. Light and edaphic factors continue to change accompanying plant succession, and the final light and edaphic conditions are established in the climax stage.

2. Characteristics of Seeds and Seedlings

The light and edaphic factors mentioned above are important when the long-term sequence of plant succession is considered. However, other factors strongly affect the progression of plant succession in the short-term sequence in early stages. Keever (1950) considered the cause of replacement of dominants in early stages of the succession of an old-field in North Carolina. She had several questions: 1) Why is horseweed, rather than some other plant, usually dominant in the first year fields ?, 2) Why does horseweed fail to hold dominance more than one year ?, 3) Why is aster delayed in assuming dominance until the second year ?, 4) Why does aster fail to hold dominance after the second year ? and 5) Why is broomsedge delayed in assuming dominance until the third year ?

She considered an orthoseral sequence of stages and noted some exceptions. These gave rise to questions such as, 1) Why are a few first-year fields clearly dominated by ragweed with almost complete absence of horseweed ?, 2) Why does aster occasionally share dominance with horseweed in first-year fields ?, 3) Why does second-year aster-dominance occasionally persist for an additional year or more ?, and 4) What effect does erosion have on the general pattern of succession ?

In the successional course there, *Andropogon virginicus* dominated for several years after the *Aster pilosus* stage, and then was replaced by the pine forest stage. Keever analysed the motive force of succession based on the characteristics of life histories of dominants and their response to environmental factors.

That the dominants in the early stages of secondary succession have strong

resistance to drought was pointed out by some researchers (Crafton and Wells 1943, Oosting and Kramer 1946, etc.). Keever also noticed *Erigeron canadensis* as being a species resistant to drought.

She particularly noticed that *Erigeron canadensis* had mature seeds early in August, germinated from the summer to the autumn without dormancy, survived and grew during the winter as rosettes, and flowered and then died until the next summer. This is an important fact in *E. canadensis* becoming a dominant in an early stage after denudation. She pointed out that a summer annual, *Ambrosia artemisiaefolia* could dominate when *E. canadensis* was removed in the first year. The dominance of *E. canadensis* as a pioneer would be related to the time of denudation. In the experiment using denuded quadrats starting each month (Numata and Ohga 1965), the denuded quadrats established during the autumn and early spring were dominated by *Ambrosia artemisiaefolia* var. *elatior*, and other quadrats established in other seasons were dominated by *Digitaria adscendens* and *Setaria viridis* (Numata 1979).

In the case of Keever, the dominant *Aster pilosus* following *Erigeron* could not germinate until the following spring, and it was difficult for the seedlings to win in the competition with *Erigeron canadensis* for light and moisture. Therefore, *A. pilosus* became dominant after the withering of *E. canadensis*, and even in the first year both could be dominant if the field was cultivated until the summer.

The seeds of *E. canadensis* matured in late autumn, however that was too late to germinate. Instead, they germinated during the following spring, but grew only 2~3 inches in height during the first year. They flowered in the second year after surviving the winter. The flower stalks withered, however basal rosettes survived and flowered in the following year. Keever clarified the fact that *A. pilosus* grows quickly under good light and water conditions. They can flower during first year under ideal conditions obtainable in a greenhouse, though this is impossible in the field.

In the meantime, *Andropogon virginicus* invaded and gradually dominated because seedlings of *Aster pilosus* could not grow in the shade and were weaker than *A. virginicus* in its resistance to drought. Even this strong species, *A. virginicus* could not dominate until the third year, because the supply of seeds was insufficient to occupy all the surface. Seeds of *A. virginicus* ripened in the late autumn; however, they did not germinate surviving the cold winter. They grew well under strong light intensity, and then became dominant after three years in old fields.

To understand the replacing phenomenon of dominants in early stages of secondary succession, characteristics of the life history of species are most important. The environmental condition developed by a dominant is not always beneficial for the following dominant, but inspite of this fact, the following invader becomes dominant (Keever 1950).

The authors (Hayashi and Numata 1967) tried to analyse the causes of plant succession, particularly of the replacement of dominants in early stages of secondary succession with ideas similar to Keever's. At first, 14 species among the constituents of the early stages of secondary succession in central Japan were

studied with emphasis on their ecological characteristics of propagules and germination. The first-year pioneers in the denuded quadrats have relatively heavy propagules having a long after-ripening period which is promoted in germination by the vernalization effect.

3. The Role of Allelopathy

Weeds found growing on arable lands are ecologically similar to pioneers in secondary succession, ruderal plants on footpaths between arable fields and aliens. One of the characteristics common to weedy species is allelopathy. This term was originated by Molisch (1937), followed by Knapp (1954), Grümmer (1955) and Rice (1974). Muller et al. (1964) defined it as "chemical plant competition" or "chemical inhibition"; however, it means chemical plant cooperation as well as competition, as Molisch already pointed out. In other words, allelopathy is "chemical plant coaction".

Regarding agricultural problems of crop rotation and soil sickness, allelopathic substances have been noticed since the time of A. P. de Candolle (1832) and J. von Liebig (1852). Bonner (1950) classified allelopathy into autotoxic and antibiotic. Related to the ecological roles of allelopathy, Deleuil (1950) who studied the shrubby heath in the Mediterranean region found that extracts from the soil of Rosmarino-Ericion had inhibited early growth after germination. Extracts from the roots of the characteristic species of the heath showed similar action. The stronger such an inhibitory action of component plants is, the higher the fidelity of plants to the alliance is. If a characteristic composition of species is established due to such a mechanism, allelopathy will be a strong basis for phytosociological phenomena.

Knapp (1954) tried to extend the idea of allelopathy to the total range of plant community ecology. The excretion of salts by guttation of halophytes and the cuticular excretion of Ca, K, Mg and P compounds are washed away by rain water and change the floristic composition of vegetation. Root exudates, for example amino acids, seem to change the floristic composition of vegetation through the enrichment of microflora of the rhizosphere. Autotoxic substances excreted from seeds during germination in relation to seeding density, and substances inhibitory or promotive to the germination of seeds of different species are known.

Grasslands of *Stipa pulchra*, *S. lepida*, *Poa scabrella*, etc. in California degenerate into annual grasslands of exotic plants, *Bromus mollis* and *Avena fatua* where aromatic shrubs such as *Salvia leucophylla* and *Artemisia californica* invade killing grasses with excreted terpens (Muller et al. 1964, 1966). This is a striking example of allelopathy affecting succession. More general examples were described by Keever (1950), Bard (1952), Rice (1964), etc. Keever explained the motive force of secondary succession on the basis of allelopathy as well as of ecological characteristics of seeds and seedlings.

At the beginning of our study, cis-dehydromatricaria ester (*cis*-DME) was separated from rhizomes and roots of *Solidago altissima* which inhibits the growth of rice seedlings. In the case of *S. altissima*, *cis*-DME was the sole growth inhibiting substance; however, *Erigeron annuus* was found to have three compounds chemically resembling *cis*-DME, namely, *cis*-matricaria ester (*cis*-ME), lachnophyllum ester (LE) and *trans*-matricaria ester (*trans*-ME) among which *cis*-ME and

LE have strong inhibitory effects. Without exception they are methyl esters of polyacetylenic α, β-unsaturated C_{10}-carboxylic acids. The presence of these esters and their derivatives in various composite species was first discovered by Sörensen et. al. (1953) and has been exhaustively investigated by Bohlman et al. (1964). Kawazu et al. (1969) reported that cis-DME has a strong inhibitory effect on rice seedlings.

In our experiment (Numata et al. 1973), seeds of *Oryza sativa*, *Miscanthus sinensis*, etc. were placed on a 0.4% agar plate containing 0.1~50 ppm of allelopathic substances. The inhibitory effect appears at between 5~10 ppm for other species. cis-DME has an autotoxic effect on the germination of *S. altissima* itself between 10~20 ppm. The antibiotic and autotoxic effects of cis-DME are very significant for maintaining the territory by vegetative propagation, inhibiting the invasion of native grasses, such as *Miscanthus sinensis*, and colonization in a new habitat not contaminated with cis-DME.

The soil was collected from a *S. altissima* growing area, and 18mg of cis-DME was extracted and identified from 3.2kg of air-dried soil. This is equivalent to 5 ppm of cis-DME the concentration of which is enough to regulate the germination or growth of competitive plant seedlings. The succession of weedy pioneer species on disturbed soils has been observed and analysed (Numata and Yamai 1955, Numata 1956, Numata and Suzuki 1958, Hayashi and Numata 1967, and Numata 1969), and it was concluded that *Ambrosia artemisiaefolia* var. *elatior* is a first year pioneer plant, and *Erigeron* spp. and *Solidago altissima* follow it. They are then replaced by *Miscanthus sinensis* in several years. The replacement of dominants is mainly caused by their own species characteristics, particularly of their seeds and seedlings (Hayashi and Numata 1967, 1968), but there is another factor that controls the progress of succession caused by allelopathic substances excreted by those pioneer plants. The communities of *Erigeron floribundus*

Table 4. Characteristics of seeds of pioneer species
(Hayashi and Numata 1967).

Species	Fresh weight/100 seed grains (mg)	Disseminule form*
Ambrosia artemsiaefolia var. *elatior*	424	D_4
Setaria lutescens	359	D_1
S. viridis	219	D_1
Polygonum nodosum	136	D_1
Rumex conglomeratus	110	D_4
R. japonicus	100	D_4
Digitaria adscendens	68	D_4
Oenothera muricata	45	D_4
Erigeron annuus	3	D_1
E. sumatrensis	3	D_1
Eleusine indica	32	D_4
Chenopodium album var. *centrorubrum*	24	D_4
Capsella bursa-pastoris	6	D_4
Veronica arvensis	11	D_4

* D_1 : anemochore; D_4 : clitochore

flourished in old fields during the second year; however, they rapidly lost vigor in the third year(Nishida and Kasahara 1975).   This fact may be caused by autotoxic allelopathy.   The allelopathic substances of *Erigeron philadelphicus*, *E. floribundus*, *E. canadensis* as well as *E. annuus* were separated and identified (Numata et al. 1975).

The above-mentioned weedy pioneer species are all aliens, naturalized in Japan, which seem to keep their predominance by the process of allelopathy.   On the other hand, some native plants dominating in the plagioseral stage might have a similar situation.   *Artemisia princeps* is a forb contained in the *Miscanthus sinensis* stage (the perennial grass stage) as a differential species; however, it becomes a dominant resulting in a plagioseral stage.   The water extracted from the underground part of *A. princeps* strongly inhibits the germination of *Digitaria adscendens*.

Caffeic acid is one of the most popular polyphenol compounds among plant products (Marby and Difeo 1973).   However, this work first clarified that it accumulates in the underground part of *A. princeps* in a high concentration (200— 250mg of caffeic acid per 1kg dry weight of rhizomes and roots) which effectively inhibits the growth of a plant.

Allelopathy is considered from the standpoint of the cause of species combination in a community, as an inhibitor in plant competition, as a cause of soil sickness, and as the motive force of secondary succession.   There are some cases where a community invades another and promotes plant succession as in the case pointed out by Muller (1964).   However, in our study on pioneer weedy species such as *Erigeron* spp. and *Solidago altissima* in secondary succession and a plagioseral species such as *Artemisia princeps*, the role of allelopathic substances excreted from those plants has a kind of negative role suppressing the progression.   The progression of succession is mainly caused by the competition of dominants based on the ecological characteristics of those species, particularly of seeds and seedlings (Hayashi and Numata 1967, 1968).

4.   The Role of Fungi

An important factor influencing the direction of plant succession seems to be fungi.   Whether a natural forest is established or not is decided by whether seedlings are infected by fungus diseases or not (Kurata 1947).   *Cryptomeria japonica* is not infected in this way by damping-off on sterile clay or sandy soils. In fact, it is often healthy even if the fungi of damping-off are dispersed on a clay plot.   However, young seedlings suffer due to fungus diseases on fertile soils with high precipitation and moisture.

According to Kurata (1947), *Larix leptolepis* is the weakest of the plantation tree species in Japan against such a fungus disease.   As a result, natural forests of *L. leptolepis* are established only on the most sterile soils such as volcanic ejects, south-facing collapsed slope, etc. where microorganisms cannot live.   *Pinus densiflora* is very similar to *L. leptolepis* in its ecological characteristics in relation to the habitat, and its natural forests are only found on sterile substrata such as ridges, sandy or clayey soils, after forest fires, and on bald hills.

Natural forests of *Abies sachalinensis* and *Picea jezoensis* in Hokkaido were sometimes damaged by typhoon.   At these times, trees that were mechanically

weak against wind pressure were fallen selectively. The weak trees were mostly those infected by fungus disease (heart rot, particularly root rot). The percentage of the damage of trees by a typhoon in a forest was 100, 70, 30, etc. depending on the occasion. The damage was mostly stems broken by the strong wind 90% of which were infected by fungous diseases. Therefore, the percentage of wind damage did not depend on the difference in the strength of wind but rather on the difference in the infestation by fungous diseases (Imazeki 1958). Fallen trees were invaded by wood-borers and completely damaged by an increase in these. Simultaneously, *Armillariella mellea* grows there. When *Abies sachalinensis* is compared with *Picea jezoensis* in its sensitivity to fungus diseases, the former seedlings are stronger and grow on the soil surface and fallen trees, but the latter are weaker and only grow on fallen trees which serve as nurse logs.

Fungus diseases and noxious insects have a close relationship to the progression of the arborescent stages of succession. This phenomenon shows succession as an ecosystem succession. The role of microorganisms, insects and other animals are, in general, closely related to the progression of succession, not only in arborescent stages, but also in herbaceous stages. The role of large grazing animals is very great in grassland succession.

III.　Theories of Succession

At this moment, the most important thing to do is to analyse causal relationships in succession. The accumulation of these analyses will lead a new theory of succession.

As ecologists know, there are main two theories of succession, monoclimax and polyclimax. Imanishi (1950) called large biomes (tundra, desert, steppe, savanna, taiga, deciduous broad-leaved forest, evergreen broad-leaved forest, etc.) the first ecosystem, and biomes within a macroclimatic area the second ecosystem. He criticized Clements' climax theory as being a polyclimax in the first ecosystem and a monoclimax in the second. Is this a logical contradiction? For Imanishi succession is an aspect of habitat segregation which is the most basic principle of ecology, although the former is a chronological and the latter is a spatial principle. Habitat segregation is caused not only by climate but also by soil, geomorphology, etc., and Imanishi's idea is common to the polyclimax theory.

There were discussions on the monoclimax vs. polyclimax theories in earlier days. After that, Whittaker's climax pattern theory was submitted on the basis of the concept of vegetational continuum. According to this idea, communities are the population complex corresponding to the environmental gradient. The concept of *vegetational continuum is common to that* of Imanishi's specific synusia and Gleason's individualistic concept.

The chronological order of coastal plant communities in a succession: sparse, unstable herbaceous communities of *Zoysia macrostachya, Calystegia soldanella,* etc.→dense stable herbaceous communities of *Imperata cylindrica* var. *koenigii,* etc.→scrub communities composed of *Rosa wichuraiana, Elaeagnus umbellata, Vitex rotundifolia,* etc.→pine forests→evergreen broad-leaved forests of *Machilus thunbergii, Castanopsis sieboldii* in central Japan is similar to spatial orientation from the coast inland, which is habitat segregation according to Imanishi. This

is a sequence based on mesophytism (from dry, sandy and halophytic to mesic and loamy habitats). Succession and habitat segregation are different principles, chronologically and spatially, and are equally basic in my opinion.

One more notable theory on succession was submitted by Hayata (1929). It was related to plant communities on Mt. Fuji. He was originally a plant taxonomist and submitted a new idea of the dynamic system of classification and participation theory. In relation to these ideas, he was very eager to study plant succession on Mt. Fuji. Most plant ecologists in Japan consider plant communities there as being immature, however he considered those as being already mature. As an example of plant succession he noticed that he could not find saplings of *Tsuga diversifolia* under a pure stand of it at about 2,000m in alt., though he found many saplings of *Abies veitchii*. He found that *Tsuga diversifolia* communities gradually became *Abies veitchii* communities. The longevity of *Abies veitchii* is rather short, and *A. veitchii* communities are replaced by *Larix leptolepis* communities after several generations. On the other hand, he observed examples of different replacement, *Abies veitchii* communities by *Tsuga diversifolia* communities, *Larix leptolepis* communities by *Picea jezoensis* var. *hondoensis* and *Tsuga diversifolia* communities, etc. As a conclusion, *Picea jezoensis* var. *hondoensis*, *Abies veitchii*, *Larix leptolepis*, *Tsuga diversifolia*, etc. are successionary equals, and the direction of replacement of those subalpine tree species is not specified. He showed concrete examples with the actual names of places on the replacement of *Abies veitchii* forests by *Larix leptolepis* forests. According to the common sense of ecology, the replacement of shade tree communities such as *Abies veitchii* by sun tree communities such as *Larix leptolepis* is not believable. However, his standpoint is close to the idea of cyclic succession (Watt 1947). A Japanese silviculturist, Terazaki (1924) noticed this fact in the forest succession.

Hayata denied the Darwinian theory of the struggle for existence and natural selection as an evolutionary theory. He explained biological diversity as an intrinsic factor, but not according to external conditions, and he constructed a dynamic system of classification. He was interested in the succession theory from the standpoint of non-natural selection. According to him, all species and communities suffer a natural death as an intrinsic factor. Then, replacement of communities and dominants was explained on the basis of the intrinsic factor theory.

Margalef (1968) discussed the relationship between succession and evolution. According to him, "evolution cannot be understood except within the framework of ecosystems. By the natural process of succession, which is inherent in every ecosystem, the evolution of species is pushed—or sucked—in the direction taken by succession, in what has been called 'increasing maturity'. The implication is that, in general, the process of evolution should conform to the same trend manifest in succession. Succession is in progress everywhere and evolution follows and is encased in the successoinal framework. As a consequence, we expect to find a parallel trend in several phylogenetic lines which can also be recognized as a trend realized in succession".

As was mentioned before, the successional trend from the herbaceous to the arborescent stages is contrary to the evolutionary trend from the arborescent to

the herbaceous forms and from perennial to annual herbs (Numata 1967). This might be related to Margalef's proposal. There are two opposite theories on the agent of succession, autogenic succession (Clements 1916) and allogenic succession (Tansley 1920). However, it depends on the definition of succession, depending, for example, on whether we can consider every vegetational change caused by upheaval and subsidence of the ground as succession, or whether we consider only vegetational development or retrogression occurring without external factors as succession. As we ascertained the phenomenon of repeating the replacement of dominants in denuded quadrats, such as *Ambrosia artemisiaefolia* var. *elatior*→ *Erigeron annuus*→*Miscanthus sinensis*, the same progressive sere was repeated in the same plots in early stages of secondary succession after denudation. Such a case is explained well with the idea of autogenic succession. We can see so-called allogenic succession with the collapse of a precipice, but the replacement of dominants in established communities after the collapse follows the principle of autogenic succession. Considering such a case, the concepts of allogenic and autogenic succession are not interchangeable.

Various problems in the causal analysis of succession are discussed, and the author hopes to establish a more comprehensive and inclusive theory of succession through the accumulation of actual data and causal analyses of various mechanisms of succession.

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