STAGE AND PHASE DYNAMICS IN EARLY STAGES OF SECONDARY SUCCESSION

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The course of plant succession was formalized by Clements (1916) and others. Descriptive and qualitative data on succession in special areas have been accumulated, however no attempt at their quantification has appeared. The degree of succession (DS) has been devised (Numata 1961), and the relationship between the biomass of a community and its dominant, and DS is shown (Numata 1974). Due to such an idea, inter-and intra-stage, and inter-and intra-phase discriminations are done for seral grasslands as well as secondary and climax forests. One seral stage has several phases.

The situation of a plant community on a seral course is quantitatively indicated using the degree of succession, DS (Numata 1969, Tsuchida and Numata 1979). DS was originally proposed as a basis for judging the quantitative condition and trend of a grassland community (Numata 1969). DS is difined as follows :

$$DS = \left[\sum_{i=0}^{n} d_i l_i / n \right] \cdot v$$

where l_i is the life span of the constituents, d_i is the relative dominance (the summed dominance ratio, SDR%), n is the number of species, and v is the ground cover ratio ($0 \sim 1$).

For example, the *Miscanthus sinensis* stage is an ordinary perennial grass stage in Japan, however it covers a range of about 600 (from 200 to 800) in DS with a peak of 500. The peak is of DS and biomass of a dominant. The former half, 200−500 in DS has an ascending trend, and the latter half, 500−800 in DS has a declining trend in the biomass of the dominant species as well as in that of the whole community (Numata 1976−Fig. 1). However, in the latter half, the biomass curve of the whole community ascends in an undulating way with the influence of the biomass of the following dominant. Sometimes, the biomass in the early stages is a little higher, and lesser, then gradually increase as shown in Fig 2.

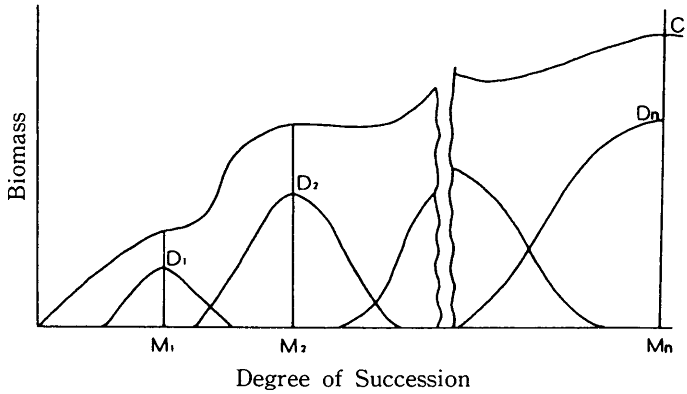

Fig.1 A schematic biomass curve of communities (C) and dominants (D_1-D_n) corresponding to DS. M_1, $M_2 \cdots$, M_n are the peaks of the DS curve of the dominant species D_1, $D_2, \cdots$, D_n respectively. The C curve does not smoothly ascend, but undulately goes upward in general. The concave parts of the C curve appear in the border between two peaks (Numata 1976).

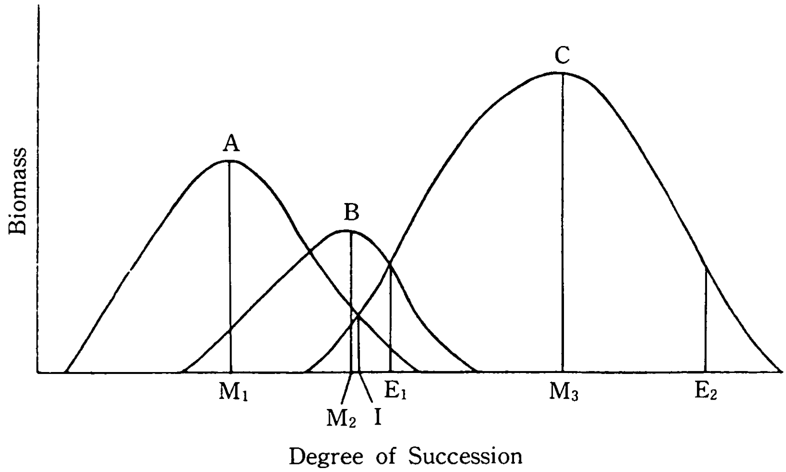

Fig.2 The biomass-DS relationship including a plagioseral stage B as well as orthoseral stages A and C.
A : *Erigeron annuus,* B : *Zoysia japonica,* C : *Miscanthus sinensis.*
M_1, M_2 and M_3 are the modes of the curves of three dominants.
I : the condition including *M.sinensis* in the *E. annuus* stage,
E_1 : Degraded condition of *M. sinensis* under grazing,
E_2 : Degraded condition of *M. sinensi* with increase of shrubs (Numata 1974).

The distinction of a seral stage from others, for example, discrimination of a *Miscanthus sinensis* stage from a *Zoysia japonica* stage, is an interstage diagnosis of grasslands. Compared with this, distinction of a phasic community from others within the framework of a *Miscanthus sinensis* stage, for example, discrimination of a phasic community with 300 in DS and another with 500 is an intrastage diagnosis of grasslands. The interstage diagnosis is not usually difficult due to recognizing the dominant species of seral stages. However, the intrastage (phasic) discrimination and diagnosis including grassland conditions and trends under the same dominant is rather difficult. For that purpose, DS was devised as an effective tool.

The idea of phase was proposed early by Watt (1947) as a regeneration complex including pioneer, building, mature and degenerating phases within a seral stage, such as brecklands and a climax stage as beech forests. In relationship to this, he proposed the idea of cyclic succession which had also been proposed by Thoreau (1893) based on his nature-loving life in a woodland (Whitford and Whitford 1951).

There are many studies on the natural regeneration of a beech forest starting from gaps (Nakashizuka and Numata 1982). In our field survey of a natural beech forest at Kiyadaira, Nagano Prefecture in Central Japan, phases 1~5 were distinguished. Phase 1 is a grassy *Sasa* phase with beech seedlings, 2 is a relatively dense young tree phase, 3 is an intermediate tree phase with vigorous growth, 4 is a mature phase with big trees300 to 400 years old, and 5 is an overmature, declining phase with oldest trees. This series of phases is sometimes considered a sere from the pioneer to the climax stage. Certainly, the phasic development is somewhat similar to progressive succession. However, a beech forest as a climax has all phases 1~5. A beech forest is a phase-complex. A climax forest is not only phase 4, but also has phases 1~3 and 5 which form a sustaining and regeneration phase-complex. Such a mosaic of various phases under the influence of a dominant, beech (*Fagus crenata*) is just a climax. The state as such is not exactly expressed by a climax being a statically stable stage, but is in dynamic equilibrium.

This kind of phasic change including retrogression as well as progression is found not only in a climax but also in every seral stage. For example, a cyclic change of phases is found even in *Miscanthus sinensis* meadows.

In our observations, seedlings of *Miscanthus* grass are frequently found on the ground after burning (if not burned, there are very few seedlings under a thick layer of litter) or in an upland field near the meadow (due to the wind dispersal of the seeds). Some of those small seedlings of a monocotyledonous type grow into tufted forms or tussocks. In central and southern Japan, tussocks grow 2 m or so in shoot height during vegetative growth and higher if their heads and stalks are included. One clump of tufted aerial shoots consists of one hundred to several hundred shoots which are sometimes densely and sometimes loosely gathered. After vigorous vegetative growth for several years, clumps have dead centers. A clump is broken into small pieces of clonal growth which are the starting points of the following generation, phase 1. That is to say, one generation of *Miscanthus* grass starting from seed dispersal is Phase 1: seedings→Phases 2～3: tufted growth developing clumps→Phase 4: vigorous vegetative growth and production of seeds →Phase 5: clumps coming to pieces with dead centers→Phase 1': seedlings in the vacant niche or the regeneration of small pieces of clones. Such a sequence of 1→2→3→4→5→1'→2→3…… is certainly a phasic change in a semi-natural meadow (Figs. 3,4). Therefore, a *Miscanthus* meadow is a regeneration complex of various phases which is very similar to the cyclical process seen in European heathland (Gimingham 1972). Thus, the cyclical phasic change is observed in seral stages as well as climax stages. The *Miscanthus sinensis* stage meadow in an orthoseral course of succession is a transitional stage between a perennial herb and a shrubby stage which procceds from phase 1 to 5 without a phasic cycle returning to 1'. However, when interference from outside, such as burning and /or mowing, stops the progressive succession from going to the following stage, a cyclical

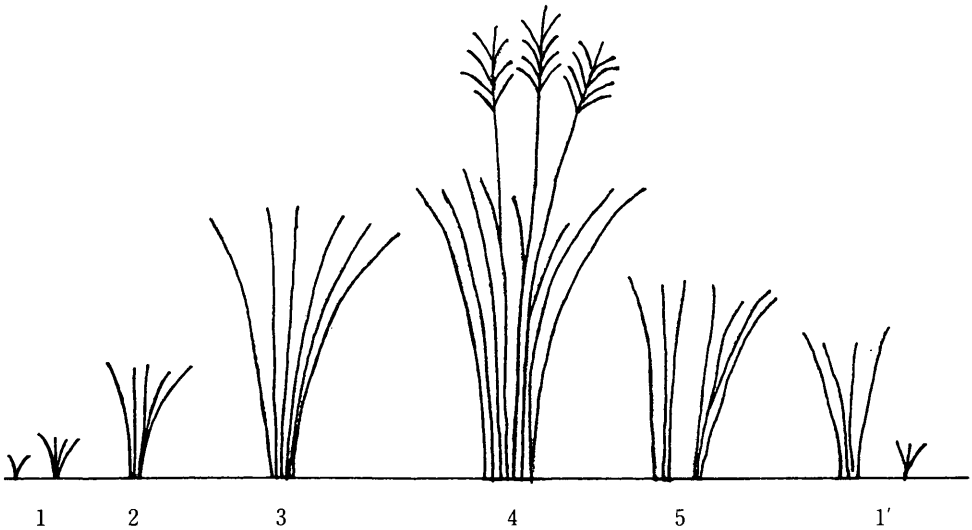

Fig.3 A sequence of growth forms of *Miscanthus sinensis* expressing a phasic change of a semi-natural meadow in Japan.

Fig. 4-1

Fig. 4-2

Fig. 4-3

Fig. 4-4

Fig. 4-5

Fig.4 The photographs of growth forms in a phasic change of *M. sinensis* meadow

4-1 Phase 2
4-2 Phase 3
4-3 Phase 4 showing clumps of the mature phase in the autumn
4-4 Phase 5 showing a dead center in the spring
4-5 Partly showing Phase 5 and 1.

phasic change will be seen. Biotic factors in a seral stage and climatic factors in a climax cause a cyclical phasic change with dynamic equilibrium.

Nevertheless, the mature phase of a meadow as a quasi-stable state is not always homogeneous. It includes patches of clumps of various phases (1~5) under the dominant

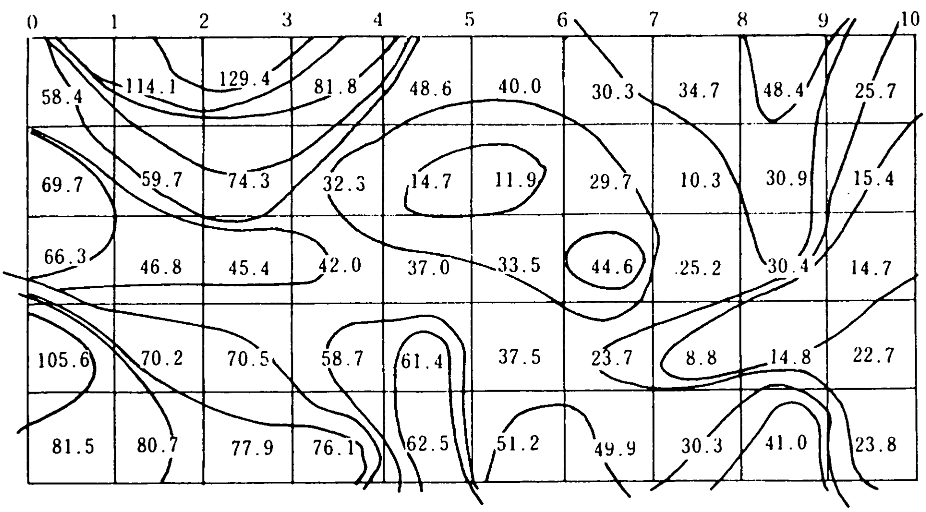

Fig.5 The DS-isogram of a pastune community (Numata 1979).

state of mature phase (4) clumps. This kind of heterogeneity is shown using the DS isogram (Numata 1979–Fig. 5).

Based on DS, the rate of succession (RS) will be calculated as follows:

$$RS = \frac{DS(t_n) - DS(t_{n-1})}{\text{Length of time (months or years)}}$$

In our experiment(Numata 1982), $\overrightarrow{RS}$ (progressive RS in month) was 1.4~4.8 in DS, and $\overrightarrow{RS}$ (progressive RS in year) was 16.2~57.6 in DS in the early stage of secondary succession. When the progressive rate of succession ($\overrightarrow{RS}$) is compared with the retrogressive rate of succession ($\overleftarrow{RS}$) between the *Zoysia joponica* pasture and the *Miscanthus sinensis* meadow, $\overrightarrow{RS}$ without grazing is slower than $\overleftarrow{RS}$ under grazing. The rate of succession in the typical soil condition (RS_{soil}) is also different from the rate of succession in vegetation ($RS_{veg.}$) (Numata 1987). Usually $RS_{veg.}$ is faster than RS_{soil}.

References (* in Japanese)

Clements, F. E. (1916) Plant Succession. Carnegie Inst. Wash. Pub. No. 242.

Gimingham, T. H. (1972) Ecology of Heathlands. Chapman & Hall, London.

Nakashizuka T. and Numata, M. (1982) Regeneration process of climax beech forest with the undergrowth of *Sasa*. I. Structure of a beech forest. Jap. J. Ecol.**32**, 57−67.

Nakashizuka, T. and Numata, M. (1982) Regeneration process of climax beech forests. II. Structure of a forest under the influence of grazing. Ibid.**32**, 473−482.

Numata, M. (1961) Some problems in the secondary succession and judging the seral condition and trend. Biol. Sci.**13**(4), 146−152.*

Numata, M. (1969) Progressive and retrogressive gradient of grassland vegetation measured by degree of succession−Ecological judgement of grassland condition and trend, IV. Vegetatio **19**(1−6), 96−127.

Numata, M. (1974) Environmental diagnosis from the viewpoint of ecology. Environment Creation **4**(1), 49−54.*

Numata, M. (1976) Ecological studies of temperate semi-natural meadows of the world −Particularly on primary production. J. Jap. Grassl. Sci.**22**, 17−32.

Numata, M. (1979) Facts, causal analyses, and theoretical considerations on plant succession. Bull. Yokohama Phytosoc. Soc. Japan **16**, 71−92.

Numata, M. (1982) Experimental studies on the early stages of secondary succession. Vegetatio **48**, 141−149.

Numata, M. (1987) Degradation of grassland ecosystems and their recovery. International Conf. on "Rehabilitation of Degraded Ecosystems:A Global Issue", 14−16 Dec. 1987, Varanasi, India.

Thoreau, H. D. (1860) The succession of forest trees. The Writings of Henry David Thoreau, Vol.**9**, Excursions (1883).

Tsuchida, K. and Numata, M. (1979) Relationship between successional situation and production of *Miscanthus sinensis* communities at Kirigamine Heights, Central Japan. Vegetatio **39**, 15−23.

Watt, A. S. (1947) Pattern and process in the plant community. J. Ecol.**35**, 1−22.

Whitford, P. and Whitford, K. (1951) Thoreau : Pioneer ecologist and conservationist. Sci. Month.**73**, 291−296.