Secondary Succession of Herbaceous Communities in Japan
—Seed Germination and Shade Tolerance of Seedlings of the Dominants—*

by

Ichiroku HAYASHI

Sugadaira Montane Research Center, The University of Tsukuba

Introduction

In a previous paper (Hayashi 1977), I described an example of secondary succession and the seed weight of constituent species of seral communities. The successional sequence of the dominant species in the ruderal and abandoned sites was as follows; *Polygonum* spp., *Echinochloa crus-galli, var. crus-galli, Chenopodium album, Setaria viridis, Ambrosia artemisiifolia* and *Digitaria adscendens* in pioneer stage; *Erigeron* spp. and *Oenothera parviflora,* in winter annual stage; *Artemisia princeps.* and *Solidago altissima* in perennial herb stage and *Miscanthus sinensis* and *Imperata cylindrica* var, *koenigii* in perennial grass stage.

In the present report, I describe the germination behaviour of seeds and shade tolerance of the seedlings of important species of herbaceous seral communities. The species names in this paper were refered to Ohwi's Flora of Japan (1972).

I. Materials and Methods

The germination rate under different temperature was determined for 45 species regarded as the important species based on field surveys. An examination of shade tolerance of the seedlings was made for *Chenopodium album, Erigeron sumatrensis, Artemisia princeps* and *Miscanthus sinensis,* which are the dominants for each seral stand.

Germination test

I collected the seeds used in the experiments from mature plants in the fields and made after-ripening of the seeds proceed by keeping them under room condition in dark for more than 60 days. One hundred sound seeds (fifty seeds in some species) were selected for use by examining seeds under binocular microscope. Seeds were sown on 0.6 percent agar medium prepared by boiling the agar with distilled water. The petridishes of 3 cm, 5cm and 10 cm in diameter were used according to the size of seeds tested.

The seeds were incubated in a thermo-regulated chamber at 10°C, 15°C, 20°C, 25°C, 30°C, and 40°C. Light was supplied from five 40W fluorescent lamps

* Contributions from Sugadaira Montane Research Center, The University of Tsukuba no. 50

fixed 50cm above the chamber. The seeds in petridishes were illuminated with light of intensity more than 5 Klux. Complete darkness was made by covering the whole petridish with the aluminum foil. A low temperature treatment in imbibed seed (stratification) was made by keeping the seeds in the chamber of 4°C for 60 days. At the same time, incubation 10°C and 15°C (non-stratification) was made to compare with the germination rate of stratified seeds. Representative species used for stratification experiment were *Polygonum lapatifolium*, *P. persicaria*, *Chenopodium album*, *Erigeron canadensis* and *Artemisia princeps*.

Table 1. The mean, standard deviation (s. d). and variation coefficient (%) of the germination rates in the chamber. 10 replications were made for each species

Species	Mean±s. d	Coefficient variation
Amaranthus patulus (Hosoaogeitoo)	95±2	2
Artemisia princeps (Yomogi)	29±6	20
Chenopodium album (Shiroza)	34±4	10
Erigeron annuus (Himejoon)	82±6	7
E. canadensis (Himemukashiyomogi)	97±4	3
Oenothera parviflora (Arechimatsuyoigusa)	76±9	12

I observed the seeds in petridishes every day and the date on which no more seedlings emerged was regarded as the final day of the germination for the experiment. The germination rate at the time was recorded as the data in this experiment. In order to check the variation of germination rate in the chamber, ten replications of 100 seeds of representative species were incubated. The result of this preliminary test given in Table 1 shows the range of coefficient of variation from 2 percent to 20 percent.

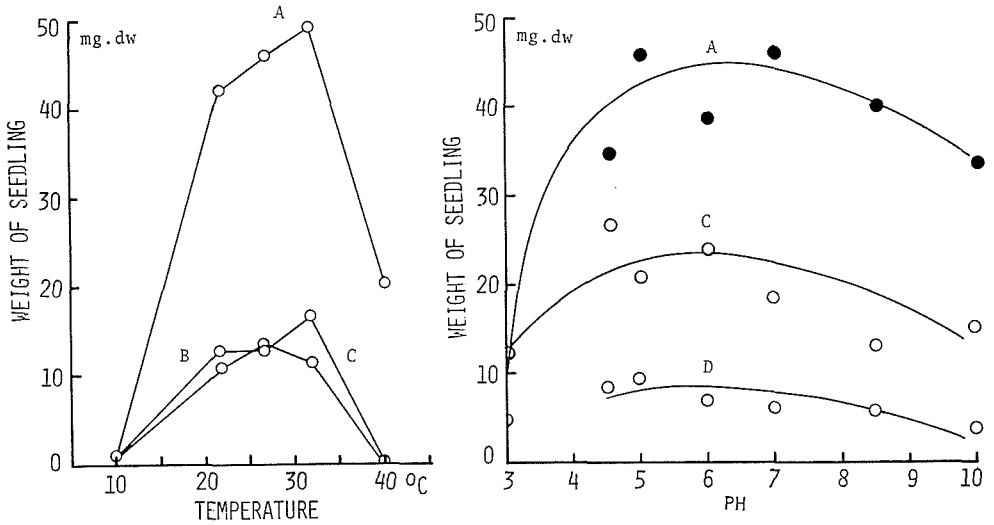

Fig. 1. Weight of seedling grown for 34 days under different temperatures and on different pH media.
A: *Polygonum persicaria*, B: *Oenothera parviflora*
C: *Chenopodium album and* D: *Erigeron canadensis*

Shade tolerance of the seedlings

Ten seeds of *Chenopodium album*, *Erigeron sumatrensis*, *Artemisia princeps* and *Miscanthus sinensis* were sown on an agar medium of 50 percent Knopp solution. Dishes were incubated at 27°C and different light intensities. The petridishes of 10cm in height and 10cm diameter were used for growth of seedlings. Various light intensities on the seedlings were obtained by covering the lids of the petridishes with black netting. The sides of petridishes were covered by aluminum foil to intercept the lateral light.

Light intensities on the seedlings in medium dishes were 11.4 Klux, 7.8 Klux, 5 Klux, 2.4 Klux, 1.2 Klux and 0.6 Klux. According to a preliminary test, the optimum growth of the seedlings occurred in the range from 25°C to 30°C at pH of 5–6 (Fig. 1). Therefore, temperature and pH medium of this experiment were maintained at 27°C and pH 6.

Seedlings were grown for 20 days after germination under continuous illumination.

The seedlings of each species were harvested and the above and below ground weight were determined. Weights were measured after drying the seedlings in an oven at 85°C for 24 hours and storing them in a desiccator.

II. Results

Germination test

As shown in Table 2 and Fig. 2, it is possible to distinguish three types of seed germination behaviour of the important species incubated under different temperatures. Maximum germination of the species occurred in three temperature ranges: 10°–15°C, 15°–30°C and 30°–40°C. The maximum germination rate of *Agropyron* spp., *Beckmannia syzigachne*, *Bromus japonica* and *Festuca* spp. oc-

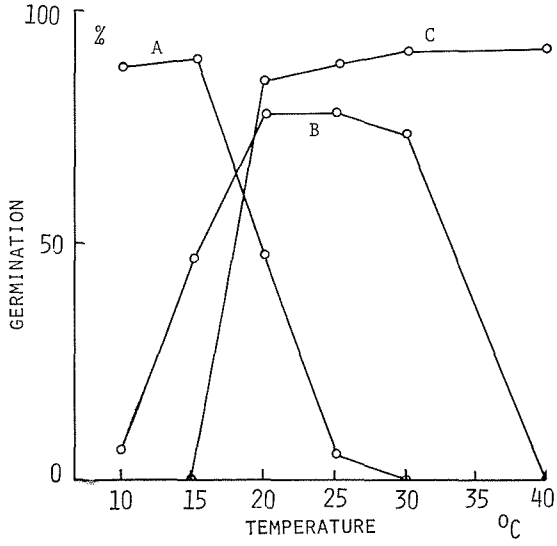

Fig. 2. Three types of germination behaviour of herbaceous species in relation to temperature
A: *Agropyron ciliare var. minus* B: *Erigeron canadensis*
C: *Digitaria adscendens*

Table 2. Germination of constituent species in successional stand of herbaceous communities. Li. and Da. are light and dark conditions in the experiment

	Germination rate (%)											
Temperature (C)	10		15		20		25		30		40	
Light condition	Li.	Da.	Li.	Da.	Li.	Da.	Li.	Da.	Li.	Da.	Li.	Da.
Polygonum lapathifolium subsp. nodosum(Ooinutade)	0	0	0	0	92	88	92	92	94	94	74	14
P. persicaria (Harutade)	3	1	1	2	76	60	90	90	80	86	84	40
Rumex acetocella (Himesuiba)	33	35	46	45	52	21	56	10	63	35	0	0
R. obtusifolius (Ezonogishigishi)	0	0	73	.	93	1	91	0	75	.	0	0
Cerastium holosteoides (Miminagusa)	0	0	16	0	4	0	0	0	0	0	0	0
Chenopodium album (Shiroza)	0	0	1	0	25	0	30	0	21	0	22	0
Amaranthus patulus (Hosoaogeito)	0	2	0	35	1	60	88	97	99	93	75	93
Chelidonium majus (Kusano-oo)	1	29	.	.	84	.	38	20	0	0	0	0
Lepidium virginicus (Namegunbainazuna)	0	0	3	3	23	4	41	10	45	4	0	0
Euphorbia maculata (OonishiKisoo)	0	0	.	.	22	10	66	.	74	40	4	0
Epilobium angustifolium (Yanagiran)	6	11	.	.	36	41	25	31	0	29	0	0
Oenothera erythrosepala (Oomatsuyoigusa)	0	0	.	.	2	0	25	1	0	0	0	0
Oe. parviflora (Arechimatsuyoigusa)	0	0	0	0	49	0	76	0	91	1	83	0
Lysimachia clethroides (Okatoranoo)	0	0	0	0	0	0	10	0	3	0	0	0
Elsholtzia ciliata (Naginatakoju)	8	0	11	0	2	0	16	.	42	.	0	0
Veronica arvensis (Tachiinunofuguri)	24	4	39	12	54	21	4	0	0	0	0	0
V. persica (Ooinunofuguri)	5	13	3	9	12	13	54	8	37	5	0	0
Plantago asiatica (Oobako)	0	0	0	0	0	0	81	0	62	1	0	0
Lobelia sessilifolia (Sawagikyo)	0	11	.	.	14	5	23	3	5	0	0	0
Platycodon grandiflorum (Kikyo)	0	0	.	.	74	19	61	.	21	3	.	.
Anaphalis margaritacea (Yamahahakogusa)	51	6	66	2	85	1	78	30	38	11	0	0
Artemisia japonica (Otokoyomogi)	0	0	3	2	16	2	42	7	18	4	0	0
A. princeps (Yomogi)	20	0	50	5	73	29	26	14	18	4	0	0
Erigeron annuus (Himejoon)	0	0	.	.	88	1	93	15	90	2	0	0
E. canadensis (Himemukashiyomogi)	6	6	47	42	78	62	78	77	74	38	0	0
E.sumatorensis (Ooarechinogiku)	0	0	.	.	91	72	78	72	81	7	0	0
Picris hieracioides (Koozorina)	1	0	.	.	42	6	54	4	0	0	0	0
Solidago altissima (Seitakaawadachiso)	90	6	85	9	95	15	88	10	77	4	45	0
Agropyron tsukushinense (Kamojigusa)	20	80	.	.	18	30	2	0	0	0	0	0
A. ciliare var. minus (Aokamojogusa)	4	88	16	90	10	48	2	6	0	0	0	0
Agrostis alba (Konukagusa)	0	3	5	11	13	23	23	10	24	36	.	.
Beckmannia syzigachne (Minogome)	52	.	18	12	12	14	0	0	0	0	0	0
Bromus japonicus (Suzumenochahiki)	40	94	72	96	0	30	0	0	0	0	0	0
Calamagrostis canadensis var. langsdorffii (Iwanogariyasu)	2	2	2	4	16	28	18	10	24	12	0	0
Digitaria sanguinalis (Mehishiba)	0	0	0	0	84	50	84	82	90	86	78	82
D. violascens (Akimehishiba)	.	.	0	0	85	96	88	87	91	91	92	82
Echinochloa crus-galli (Inubie)	0	0	0	0	72	17	85	55	87	28	79	33
Eleusine indica (Ohishiba)	0	.	0	35	0	54	25	66	24	53	9	0
Eragrostis ferruginea (Kazekusa)	52	40	59	28	70	40	80	50	75	68	93	36
Festuca elatior (Hirohaushinokegusa)	50	68	36	88	32	68	56	48	28	26	0	0
F. ovina (Ushinokegusa)	48	58	77	55	29	55	1	1	0	0	0	0
Miscanthus sinensis (Susuki)	0	0	64	72	94	90	92	86	88	84	0	0
Muhlenbergia japonica (Nezumigaya)	0	0	.	.	30	0	17	0	.	.	.	.
Pennisetum alopecuroides (Chikarashiba)	0	0	0	0	24	4	12	88	16	12	0	0
Sporobolus indicus var. purpureo-suffusus (Nezuminoo)	0	0	0	0	42	0	43	0	31	0	22	0

curred in the range from 10°C to 15°C.

Most of dominants in the seral stands germinated in maximum rate in the range from 15°C and 30°C. *Digitaria adscendens*, *Echinochloa grus-galli* var. *crus-galli*, however, germinated at higher temperatures.

Teble 3. Percent germination of the dominant species in different pre-treatment temperatures before incubation

Temperature in pre-treatment (°C)	4		10		20	
Temperature in incubation (°C)	15	25	15	25	15	25
Polygonum lapathifolium						
light condition	0	90	0	80	0	0
dark condition	0	29	0	1	0	0
P. persicaria						
light condition	0	33	0	17	0	0
dark condition	0	21	0	1	0	0
Chenopodium album						
light condition	2	3	28	16	6	39
dark condition	0	0	0	0	0	0
Erigeron canadensis						
light condition	66	79	49	31	50	90
dark condition	3	3	12	5	5	63
Artemisia princeps						
light condition	76	67	62	78	53	50
dark condition	37	67	4	58	28	22

As shown in Table 3, stratification increased the germination rate of *Polygonum* spp., the dominant species in pioneer stage (Kunimi et al. 1960, Timson 1965, Hayashi and Numata 1967).

Light illumination increased the germination of *Erigeron* spp. and *Artemisia princeps* as well as many other species. The seeds of *Miscanthus sinensis* germinated both under light and dark conditions. (Table 2).

Shade tolerance of seedling

Table 4 shows the results of the examination of shade tolerance of the seedlings of *Chenopodium album*, *Erigeron sumatrensis*, *Artemisia princeps* and *Miscanthus sinensis*.

The seed weight was 0.473mg in *C. album*, 0.022mg in *E. sumatrensis*, 0.084mg in *A. princeps* and 0.453mg in *M. sinensis*. The weight of seedling grown from these seeds for 20 days at 27°C and 11.4 Klux was, 10.5mg for *C. album*, 0.5mg for *S. sumatrensis*, 7.6mg for *A. princeps* and 10.9mg in *M. sinensis*. The ratio of the seedling weight to seed weight was 22.1 for *C. album* 22.7 for *E. sumatrensis*, 90.5 for *A. princeps* and 24.1 for *M. sinensis*. On the other hand, this ratio under light condition of 1.2 Klux in the same temperature condition was as follows: 0.4 for *C. album*, 4.5 for *E. sumatrensis*, 2.9 for *A. princeps* and 1.1 for *M. sinensis*.

Under this light intensity, the seedlings of *C. album* decreased in weight by 60 percent of the seed weight after 20 days, while the weight of the seedlings of *E. sumatrensis* and *A. princeps* better tolerate the gloom condition than that of *C. album* and *M. sinensis*.

Table 4. Seedling weight and the ratio of seedling weight to seed weight grown for 20 days under various light intensities at 27°C for each dominant species in seral stands

Light intensities (Klux)	11.4	7.8	5.0	2.4	1.2	0.6	Seed weight (mg. dw)
Chenopodium album							
Seedling weight (mg. dw)	10.5	10.6	3.2	2.6	0.2	0.14	0.473
Seedling weight/seed weight	22.1	22.4	6.7	5.5	0.4	0.3	
Erigeron sumatrensis (mg. dw)							
Seedling weight (mg. dw)	0.5	0.7	1.3	0.4	0.1	0.04	0.022
Seedling weight/seed weight	22.7	31.8	59.0	18.2	4.5	1.8	
Artemisia princeps							
Seedling weight (mg. dw)	7.6	6.1	3.7	1.2	0.2	0.10	0.084
Seedling weight/seed weight	90.5	72.6	44.0	14.3	2.9	1.2	
Miscanthus sinensis							
Seedling weight (mg. dw)	10.9	9.8	6.0	2.0	0.5	0.44	0.453
Seedling weight/seed weight	24.1	21.6	13.2	4.4	1.1	1.00	

Table 5. Ratio of above ground weight to total weight of the seedlings of the dominant species in seral stands

	Above ground weight/total weight		
Light intensities (Klux)	11.4	7.8	5.0
Chenopodium album	0.81	0.81	0.82
Erigeron sumatrensis	—	—	0.89
Artemisia princeps	0.75	0.75	0.74
Miscanthus sinensis	0.75	0.72	0.75

It the case of *E. sumatrensis*, the maximum growth of the seedlings was observed at light intensity of 5 Klux and the growth was inhibited by higher light intensities (7.8 Klux and 11.4 Klux). Although the seed weight of *E. sumatrensis* and *A. princeps* is lighter than that of *C. album* and *M. sinensis*, rapid growth under bright conditions as well as great shade tolerance are characteristic of these species.

Table 5 shows the ratio of above-ground part to total weight of seedling for each species grown under 11.4 Klux, 7.8 Klux and 5.0 Klux, respectively. The ratio was 0.81–0.89 in *Chenopodium album* and *Erigeron sumatrensis*, 0.74–0.75 in *Artemisia princeps* and 0.72–0.75 in *Miscanthus sinensis*, respectively.

The ratio of above-ground weight to total weight of *C. album* and *E. sumatrensis* is greater than that of *A. princeps* and *M. sinensis*.

III. Discussion and Conclusion

The dominant species of herbaceous communities developing from summer to autumn in Japan, show the maximum seed germination rate in the range from 15°C to 30°C.

The optimum range of temperature for germination, however, is 10°C–15°C for the dominants in the stands initiated from autumn to winter such as *Beckmannia syzigachne*, *Agropyron* spp., *Stellaria media* and *Capsella bursa-pastoris* Some of the dominants of pioneer stage such as *Polygonum* spp., *Setaria viri-*

dis and *Ambrosia artemisiifolia* require the stratification before incubation for their germination (Hayashi and Numata 1976, Bazzaz 1970, Pickett and Baskin 1973).

The seeds of *Digitaria adscendens*, one of the pioneer species, however, do not require the stratification for germination. The germination rate of *Erigeron* spp. and *Artemisia princeps*, which dominate the winter annual stage and perennial herb stage, increased significantly with light illumination.

The seeds of *M. sinensis* are able to germinate without stratification and light illumination.

We may conclude that the seeds of the dominants of pioneer stage having the heavy seeds (Hayashi 1977) require a stratification for germination with a few exceptions (*Digitaria adscendens* and *Chenopodium album*).

According to Watanabe and Hirokawa (1974), however, stratification increases germination of *C. album* in their materials collected in Hokkaido, although an increase of germination of the species was not observed in this study. In many pioneer species, heavy seeds, which exhibit seed dormancy and have a requirement for stratification for germination are characteristics of the early life history of these species. Other species, however, such as *Erigeron* spp., *Artemisia princeps* and *Solidago altissima* produce light seeds which have no dormancy but in which germination is enhanced by illumination.

In general, the weight of the emergent seedling is propotional to the seed weight of the species. The ratio of seedling weight to seed weight, however, is greater in *E. sumatrensis* and *A. princeps* than in *C. album* and *M. sinensis*. A comparison of shade tolerance among these species shows that the seedlings of *E. sumatrensis* and *A. princeps* are able to tolerate under shaded condition whereas *C. album* and *M. sinensis* tolerate brighter and intermediate conditions, respectively. The early life history features of *E. sumatrensis* and *A. princeps* include light seed weight, an illumination requirment for germination and strong shade tolerance of seedling. *E. sumatrensis* is distinguished from *A. princeps* by its larger ratio of above ground parts to total weight of seedlings. *C. album*, *Polygonum* spp, and *Ambrosia artemisiifolia* are characterized by heavy dormant seeds and weak shade tolerance (Hayashi and Numata 1967). These seeds may exist as buried seeds in soil for long time if they do not experience the cold temperature and site disturbance conditions neccessary for germination (Pickett and Baskin 1973).

The growth (seedling weight/seed weight) of seedling of *A. princeps* and *M. sinensis* differ but the distribution of assimilated matter to above-and underground parts is similar. These species exhibit life history attributes including seed germination behaviour, growth characteristics and seed production which enable them to dominate early seral stages.

Acknowlegement

I would like to acknowlege the continuing guidance and encouragement of Dr. Makoto Numata, professor of Chiba University and Dr. Hirosi Ito, emeritus professor of Tokyo Kyoiku University.

Thanks are due to Dr. D. J. Raynal, State University of New York for

his critical reading of the manuscript.

摘　　要

草本群落遷移のメカニズムを説明するために，各遷移段階の構成種の生活様式を比較した。この報告では，各群落の構成種と優占種の発芽と芽生えの耐陰性を比較した。

1) 各ステージの群落を構成する主な種類はカモジグサ属のように種子集団の発芽率のピークが10°C(5 C)～15°Cにある種類とススキなどのように15°C～30°Cおよびメヒシバなどのように30°C～40°Cにある種類の三つのグループに分けられることが明らかとなった。

各ステージの優占種の多くは15°C～30°Cで高い発芽率を示したが，冬から初夏の群落で優占する種類では10°～15°Cで高い発芽率を示した。

また先駆群落の優占種の一つであるハルタデなどは発芽にとって低温の前処理が有効であった。多くの種で光照射が発芽率を高めたが，ヒメジョオン属ではとくに顕著であった。

2) 先駆群落の優占種は芽生えの耐陰性が小さく，それに対してオオアレチノギク，ヨモギでは耐陰性が大きかった。

芽生えの全重量に対する地上部重量の比はシロザ，オオアレチノギクで大きく，ヨモギ，ススキで小さくなった。

3) ヒメジョオン属の種についていえば，軽い風散布の種子は新しい立地に到達し易いという利益と立地に到達した後には小さな（種子が小さいから）芽生えしか作れないという不利益がある。この不利益を，芽生えの強い耐陰性という生態的形質で補償していると考えることができる。こうして種の生活様式の特徴があらわれてくる。

References

BAZZAZ, P. A. 1970. Secondary dormancy in the seeds of common ragweed *Ambrosia artemisiifolia*. Bull. Torry Bot. Club, **97**: 302–305.

HAYASHI, I. 1977. Secondary succession of herbaceous communities in Japan. Jap. J. Ecol., **27**, 191–200.

HAYASHI, I. and Numata, M. 1967. Ecology of pioneer species of early stages in secondary succession I. Bot. Mag. Tokyo, **80**: 11–22.

KUNIMI, S., Yokohama, Y. and Ishikawa, S. 1960. A method of promoting germination of weed-seeds and its application to afforestation. Prechilling and subsequent drying. Journ. Jap. Forest. Soc. **42**: 415–416

OHWI, J. 1972. Flora of Japan. 1560, Shibundo, Tokyo.

PICKETT, S. T. and Baskin, J. M. 1973. The role of temperature and light in the germination behaviour of *Ambrosia artemisiifolia*. Bull. Torry Bot. Club, **100**: 156–170

TIMSON, J. 1965. Germination in *Polygonum*. New Phytol. **64**, 179–186.

WATANABE, Y. and Hirokawa, F. 1974. Ecological studies on the germination and emergence of annual weeds I. Effect of temperature on the dormancy-breaking in seeds of *Chenopodium album*, *Echinochloa crus-galli* var. *pruticola* and *Polygonum lapathifolium*. Weed Research, **17**: 24–28.