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Ecology of Pioneer Species of Early Stages in Secondary Succession I.

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Abstract

Autecological studies were carried out about 14 important species which constitute the early stage of subsere. The comparative study of their germination behaviour is an attempt to account for the mechanism of plant succession in Kantô district, central Japan. The seed of *Ambrosia elatior, Erigeron annuus, Chenopodium album* var. *centrorubrum*, etc. were incubated under different light-temperature regimes, after preservation under three distinct conditions: 1) under room temperature, 2) stratification at 0-3°, 3) buried in the field soil. The weight of seed and their dissemination type of these species were examined, too. The seed of the pioneer species such as *Ambrosia elatior, Setaria viridis* and *Polygonum nodosum* are heavy, and the germination is characterized by: 1) slow progression of after-ripening, 2) acceleration of it by stratification at 0-3° or burying in the field. In the contrast with them, *Erigeron annuus* and *E. sumatrensis* which replace the pioneer species and become dominant of the community with the progress of succession, have light seed and high germination rate even in a younger age of after-ripening. Also they show no effect on the germination rate after stratification or burying treatment in the field soil. The characters necessary for the pioneer species in the first year are discussed based on the results mentioned above.

Introduction

The actual course of succession where plant communities establish in bare grounds and develop especially according to autogenic action has been studied in detail by one of the authors and his collaborators (Numata *et al.*, 1955[1], 1956[2], 1957[3], 1958[4], 1961[5,6], 1962[7], 1964[8], 1965[9,10]) on early stages of the secondary succession and on the ecological gradient of grassland and bamboo forests. These studies elucidated the mechanism of plant succession mainly based on the floristic composition, the age distribution of constituents, and so forth. Recently Numata has tried to measure the degree of succession by an index DS (Numata, 1961[5,6], 1962[7]). Further, the buried seed population in the soil was studied as an important basis of successional analysis and the correspondence between the plant communities and the buried seed population at the same places was discussed (Numata *et al.*, 1964[11,12], Hayashi and Numata, 1964[8]).

In this report, autecological discussions of pioneer species are made concerning the seed germination of 14 important species as the member of early stages of the subsere. The seed is essentially a nodus stage in the life history of plants as sporophyte and plants make a cycle from one generation to another through such

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a nodus. The seed population produced by a plant can be regarded in a sense as a stage of continuously growing individual from a generation to another. The niche of constituents in a plant community will be influenced by the eco-physiological behaviour of seeds and by the difference of their response to environmental conditions. Comparative studies on eco-physiological behaviours of seeds of pioneer species in the secondary succession will contribute to the knowledge concerning the establishment and development of particular plant communities starting from the bare ground. However, only the study on seed germination is not enough to explain phenomena of succession, and the further study on the response of seedlings and mature plants to environmental conditions and that on the interspecific interaction are necessary for it. We have good example of experimental sociology of seedlings (Knapp, 1954[13]) and allelopathic study on the inhibition of nitrogen-fixation by seed plant (Rice, 1964[14]) and the eco-physiological study along this line will be very important for our subject of study, too.

Method and Materials

The experimental materials were collected in the suburbs of Chiba City. *Ambrosia elatior*, as a dominant pioneer species on the soil disturbed in winter, and *Setaria viridis* and *Digitaria adscendens* as dominants on the soil disturbed on May or early summer were used for this experiment. *Oenothera muricata, Polygonum nodosum, Erigeron annuus, E. sumatrensis, Chenopodium album, Amaranthus retroflexus*

Table 1. Characteristics of seeds of species used for the experiment.

Species (Japanese name)	Fresh weight/100 seed grains (mg)	Disseminule form*
Ambrosia elatior (Butakusa)	424	D_4
Setaria lutescens (Kin-enokorogusa)	359	D_1
S. viridis (Enokorogusa)	219	D_1
Polygonum nodosum (Ooinutade)	136	D_1
Rumex congromeratus (Arechi-gishigishi)	110	D_4
R. japonicus (Gishigishi)	100	D_4
Digitaria adscendens (Mehishiba)	68	D_4
Oenothera muricata (Arechi-matsuyoigusa)	45	D_4
Erigeron annuus (Himejoon)	3	D_1
E. sumatrensis (Ooarechi-nogiku)	3	D_1
Eleusine indica (Ohishiba)	32	D_4
Chenopodium album var. *centrorubrum* (Akaza)	24	D_4
Capsella Bursa-pastoris (Nazuna)	6	D_4
Veronica arvensis (Tachi-inunohuguri)	11	D_4

* D_1, anemochore; D_4, clitochore

and *Eleusine indica* were also examined (Table 1). These are common species appeared in early stages of the secondary succession in Japan except northern Hokkaido, and autecological studies of these species will serve to solve the mechanism of establishment and development of pioneer plant communities. The seeds used for the experiment were prepared without distinction of size, form and weight, but only immature seeds were excluded. As a comparative study on the behaviour of seed germination, the preparation is carried out for each species with the same procedure.

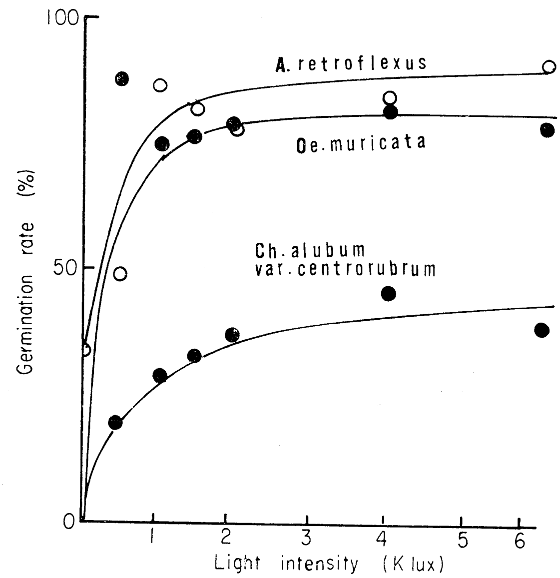

Fig. 1. Relationship between germination rate of three species and light intensity.

100 seed regains of each species were held on the 0.7 per cent agar-agar in the share under certain temperatures and illuminating conditions. The seedlings were counted at regular intervals after the seeding and the time any seedling does not appear is considered "the last day of germination" of the seed population. The light intensity was kept in 2,000 lux except particular cases (Fig. 1). The figure shows that the germination rate (%) of each species become almost constant at 2,000 lux in the light intensity. The dark treatment was applied by packing with a black thick paper soon after the incubation and it was held in the incubator in a certain period. The data used for discussion were those obtained in the range of fluctuation of $\pm 1°$. The low temperature treatment (0°-3° stratification) was applied to seeds in a Petri dish filling the agar-agar solution covered by the Alminium case in the refrigerator with the thermostat. The fluctuation of temperatures was $\pm 1°$ and $\pm 2°$ during the stratification of 2°, 10° and 15° respectively. In case of the treatment in the field soil, the seeds on the agar-agar solution in the Petri dish were packed by the tin foil and kept 1-3 cm deep in the soil and their germination was tested at regular intervals. The burying-in-soil experiments started on 12th February 1963, and the seed population was kept in natural temperatures from February to September in the field under the complete darkness and full supply of water.

Preliminary Experiment

For comparative studies of the germination behaviour and the germination rate of seed of each species, preserved conditions of seed, environmental factors for germination and the time of incubation are most important. The seed germination in the ecological sence is limited by the conditions as follows: 1. the age of seeds after harvesting, namely, the after-ripening age of seeds, 2. environmental factors for seed germination, e.g., light, temperature, O_2, water, etc. and 3. the time of incubation.

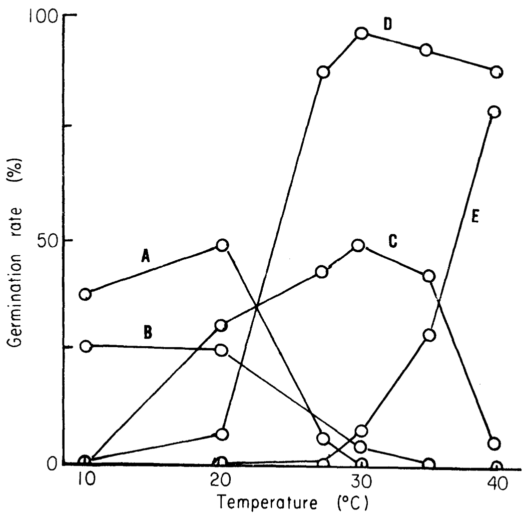

Fig. 2. The temperature requirement for germination of each species as follows: A. *Setaria lutescens*, B. *Capsella Bursa-pastoris*, C. *Digitaria adscendens*, D. *Amaranthus retroflexus*, and E. *Eleusine indica*. The days after harvesting of species A, C, D and E, and B are 192 and 330 respectively.

The germination rate of certain species must described with days after harvesting (strictly speaking, days after the fertilization of embryos) and environmental factors for the germination. In the experiment the after-ripening age of seeds was measured in days (or weeks) stored under the room condition after harvesting of each species. Differences of the germination rate according to the after-ripening age and the variation of temperature are shown in Table 2 and Fig. 2. These facts indicate that the germination rate varies with the time of fertilization and the temperature factor. Further there are some physiologically different groups of seeds corresponding to the pollinating and fertilizing time. Then, if seeds are devided according to the after-ripening age, a definte age distribution of seeds will be noticed. In Table 3 the variation of germination rate during a period is shown. It

Table 2. Germination rate of species according to after-ripening age and incubation temperature.

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 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 3. Variation of the germination rate of two *Erigeron* species in course of time.

Species \ Days after seeding	Germination rate (%)					
	0–2	2–4	4–8	8–12	12–16	16–20
Erigeron annuus	0	14.5	41.5	22.5	4.0	1.0
E. sumatrensis	44.0	33.0	6.5	2.0	1.0	1.0

Table 4. Relation between germination rate and after-ripening age at the beginning of stratification (0–3°).

After-ripening age (days)	40	60
Species	Germination rate (%)	
Ambrosia elatior	50	98
Setaria viridis	22	62
Oenothera muricata	82	84
Chenopodium album var. *centrorubrum*	45	62
Capsella Bursa-pastoris	74	71

means that differences of the after-ripening age appear as the germination rate.

If it is accerelated by the stratification, it depends on the degree of after-ripening at the time exposed to the low temperature as shown in Table 4. Owing to the preliminary experiment mentioned above, the seed germination rate can be shown only by relative values, and the spatial and time factors affecting the seed germination must be examined. The seeds used for the experiment for interspecific comparison are of the same after-ripening age and the seeds used for stratification and for the burying-in-soil treatment are of 7 and 17 weeks after harvesting respectively. The other data are described with each after-ripening age. The seeds had been kept under the room condition till the treatment was begun.

Results

The interspecific dominant-subordinate hierarchies among the constituents of a plant community were discussed by one of the authors (Numata *et al.*, 1956[15], 1954[14], 1955[1]) based on the theory on the no. of individuals-rank of species relation (Motomura, 1932[17], 1947[18]), etc. But such an interspecific relationship is recognized not only for the dominant-subordinate hierarchies in a community but also for the rank of seed weight in a buried seed population appeared in a stage of secondary succession (Fig. 3). The weight of seeds is of 100 seed grains randomly collected from mature plants. The pioneer species, such as *Ambrosia elatior*, *Setaria viridis*, *Polygonum nodosum* and

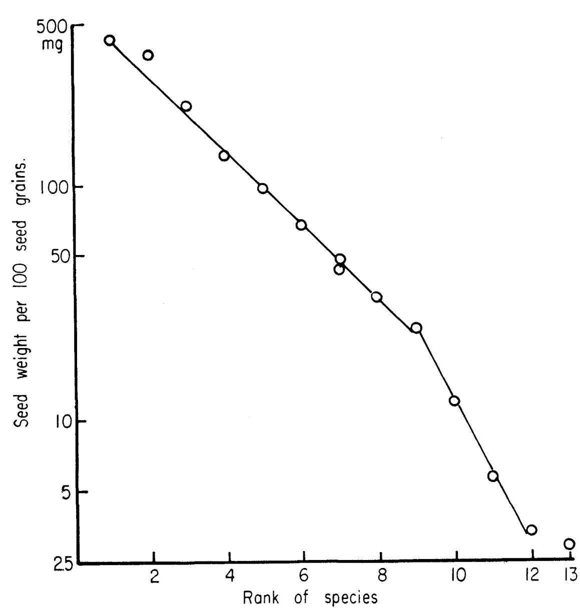

Fig. 3. The [weight of seed-grains]-the [rank of species] relation in a buried-seed population appeared in the pioneer stage of the secondary succession.

Digitaria adscendens have much greater seed weight, followed by *Oenothera muricata, Chenopodium album,* and *Amaranthus retroflexus.* The seed of *Erigeron* has the weight 1/70-1/140 of *Ambrosia elatior* and *Setaria viridis* (Table 1). The disseminule forms (Numata, 1942[19]) of these species are shown with the seed weight in Table 1. And the differences of the germination rate according to various conditions of preservation before the incubation are shown in Table 5. The pre-treatment periods are shown as the weeks in treatment under various coditions and they do not mean the weeks of incubation.

The germination test with various pre-treatments was carried out under the temperatures of 22° and 30° and light intensity of 2000 lux. In the column of species name in Table 5, five summer annuals which dominate as pioneer species in the old field succession* in the middle of Japan are shown on the top. The following species from *Erigeron annuus* to *Oenothera muricata* are dominants in the next stage (also the pioneer stage in a wide sense). *Amaranthus retroflexus* and *Chenopodium album* grow as well in the roadside as in the arable land, but never become dominant in any early stages of such secondary succession, and become dominant rarely under a particular environment. The seeds of *Chenopodium album* are considered to be buried enormously in the soil of stages of secondary succession. *Capsella Bursa-pastoris* and *Veronica arvensis* are shown as typical wayside plants. To examine the germi-

Table 5. 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	Under room condition			0°-3° stratification			In field soil at 1-3 cm depth			
Species / Weeks*	7	14	27	4	8	20	4	10	20	30
Ambrosia elatior	0	18	27	8	50	96	64	**	**	**
Setaria lutescens	0	0	0	0	0	46	12	70	**	**
S. viridis	0	1	1	0	22	50	32	62	**	**
Polygonum nodosum	—	25	19	—	—	—	69	62	—	**
Digitaria adscendens	82	57	49	—	—	—	—	—	—	—
Erigeron annuus	58	73	79	73	64	73	72	81	75	70
E. sumatrensis	75	62	75	82	74	58	85	100	48	83
Oenothera muricata	85	88	83	67	82	85	—	89	75	75
Eleusine indica	3	5	8	0	0	0	0	1	1	6
Chenopodium album var. *centrorubrum*	24	40	25	27	45	18	79	94	64	69
Amaranthus retroflexus	32	86	97	2	22	3	4	74	98	21
Capsella Bursa-pastoris	0	0	4	83	74	27	55	—	—	0
Veronica arvensis	—	—	—	—	—	—	57	—	31	14

* Number of weeks stored under various conditions.

** Seedlings decayed during the period in the soil after germinating under the dark condition with natural temperatures. The seeds of *Erigeron* and other similar species germinate only when the seeds were removed into the temperature and light conditions of 30° and 2,000 lux.

* These species usually appear on the soil disturbed from autumn to next spring (mainly in winter). (Numata *et al.*, 1955[1], 1956[2]).

nation type of each species, the germination rate was compared after the storage under various conditions, such as a dry storage under the room condition, low temperature treatments and the treatment buried in the field soil at 1-3 cm depth during winter.

The figures in the second column in Table 5 show the days of storage and treatments. The asterisks in the third column indicate that the seedling decayed during the buried period after germinating under the dark condition with natural temperatures. According to the experimental results, the pioneer species except *Digitaria adscendens*, need long periods of after-ripening to obtain high germination rates. For example, the *Ambrosia* seeds germinate only 27% even in 190 days after harvesting. The *Setaria* seeds fail to germinate and the *Polygonum* seeds germinate only 25% even in 100 days after harvesting. On the contrary to these species, *Erigeron annus, E. sumatrensis* and *Oenothera muricata* show 58-85% in the germination rate in 50 days after harvesting. *Chenopodium album, Amaranthus retroflexus* and *Digitalia abscendens*, whose germination rates increase or fluctuate according to the after ripening, show the germination rate of 24, 32 and 82% respectively in 50 days after harvesting. *Eleusine indica* and *Capsella Bursa-pastoris* show very low germination rate under the condition of 22° and 2,000 lux. In contrast to those, the seed population of pioneer species with the low temperature treatment and with the burying-in-soil treatment shows strongly accerelated germination compared with the seeds stored under the room condition. For instance, when the seeds were stored under the room condition during 190 days, the *Ambrosia* seeds give only 27% germination, and *Setaria viridis* and *S. lutescens* fail to germinate.* However in the low temperature treatment of 140 days, the *Ambrosia* and *Setaria* seeds have 96% and 46-50% germination respectively. And the seeds buried in the field soil for 70 days at 17 weeks after harvesting have over 64% germination in *Ambrosia elatior*, 62% and 70% in *Setaria viridis* and *S. lutescens* respectively, and 62% in *Polygonum nodosum*. In case of burying over 130 days in the field soil, most of the seeds of the pioneer species mentioned above germinated in the soil and all the seedlings withered. The fact indicates that the seeds of the pioneer species germinate even in the entirely darkness when the enough water and adequate temperature are given. Meanwhile *Erigeron annuus, E. sumatrensis, Oenothera muricata*, etc. as pioneer species of the second stage which dominate by taking the place of pioneer species of the first stage corresponding to the progression of secondary succession, give a high germination rate even in younger age of after-ripening, and are not much affected by the low temperature treatment and the burying-in-soil treatment. It is an interesting fact that the seeds of pioneer plants germinated on the field soil at 70 days after burying in February, 1963 but the seeds of other species could not germinate under natural temperatures of April, May and June in 1963 with sufficient water supply and they germinated only when the condition of 22° and 2,000 lux was applied. The germination of *Chenopodium album* is accerelated by the burying-in-soil treatment, but not by the low temperature treatment (i. e. continuous exposure to low temperature). The germination of *Amaranthus retroflexus* is inhibited by both of these treatments. The germination of *Capsella* seeds was accerelated by an adequate period of the low temperature treatment. *Digitaria adscendens* as one of pioneer species give a high germination rate even in a young age of after-ripening. According to these facts mentioned above, the species listed as pioneer plants

* The seeds of *S. viridis* give 50% germination at 20° in 190 days of after-ripening age.

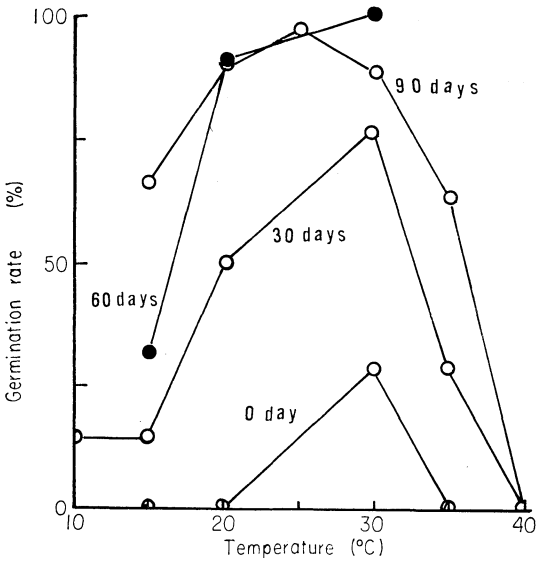

Fig. 4. Increase of the germination rate of *Ambrosia* seeds according to applying the stratification during a certain period. The after-ripening age at the time exposed to the low temperature is 175 days.

except *Digitaria adscendens* increase slowly their germination rate with the progress of after-ripening and they have rapidly high germination rates by the pre-treatment under low temperatures. On the contrary, the species such as *Erigeron annuus, E. sumatrensis, Oenothera muricata, Eleusine indica* and *Amaranthus retroflexus* do not have any accerelation effect by the pre-treatment of natural low temperatures with burying in the field soil. The applying of low temperature to the germination of a seed population prior to the incubation will be discussed in detail related to *Ambrosia elatior* as an example. The germination rate of *Ambrosia* seeds which varies according to various temperatures in the incubation even in the same age of after-ripening is shown in Fig. 4 with various durations of 0°–3° stratification. It is shown by the coordinates of the temperature during incubation and the germination rate. The figures indicates that the stratification accerelates the germition in longer duration of low temperature. From the evidence, the *Ambrosia* seeds can be expected to germinate rapidly in early spring prior to any other species. Various effects of the difference of temperatures in the stratification and in the incubation to the germination rate of the *Ambrosia* seeds are shown in Fig. 5.

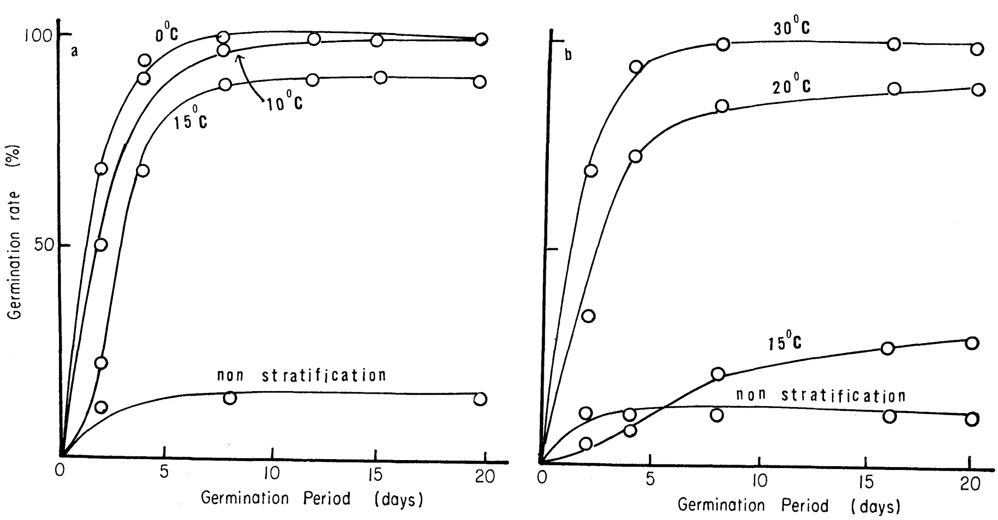

Fig. 5. Differences of the germination behaviour of *Ambrosia* seeds according to a, temperature during stratification of 60 days, and b, temperature during incubation after 0°–3° stratification of 60 days. The after-ripening age at the time exposed to the low temperature is 85 days.

The germination period and germination rate are indicated on the abscissa and the ordinate respectively. The temperatures during the stratification are 0°-3°, 10° and 15° and those during the incubation are 15°, 20° and 30° under the light intensity of 1,800 lux. It is interpreted from these results that in the range from 0° to 15° the lower the temerature during the stratification goes down, the higher the germination rate becomes (Fig. 5a). The Fig. 5b shows the result of germination of seeds under the incubation of 30°, 20° and 15° respectively after keeping them in 0°-3° during the stratification of 60 days. It is clear that in the range from 15° to 30° the higher the temperature during the incubation is, the higher the germination rate becomes. From the two evidences mentioned above, the lower the temperature during the stratification and the higher the temperature during the incubation are, the higher the germination rate becomes. From the ecological view point on the seed germination, the time necessary to obtain a certain germination rate is closely related to the ecological status of species in a plant community. Fig. 5 indicates that the time to obtain the 100% germination is shorter in cold-treated seeds than untreated ones. In other word, the seed population of *Ambrosia elatior* had the nature of "volley" of germination by the stratification. The "volley" phenomenon of germination increase according to rising temperature in the incubation. The germination behaviour of the species in a certain period was examined too. The mode of germination and the temperature requirement for germination of two species, *Erigeron annuus* and *E. sumatrensis* which are entirely the same in the growth form of mature plants and the seed weight, are shown in Fig. 6. *E. annuus* gives a high germination rate at 27° and has the elapse of 20 days untill the 80% germination. *E. sumatrensis* differs from *E. annuus* in the germination behaviour and its germination is induced in a wide range of temperature (i. e. 10°-30°) and 80% germination is obtained only in 4 days. These differences are also found among other closely related species and further investigations will be necessary to analyse these phenomena and effect to the later growth in a community.

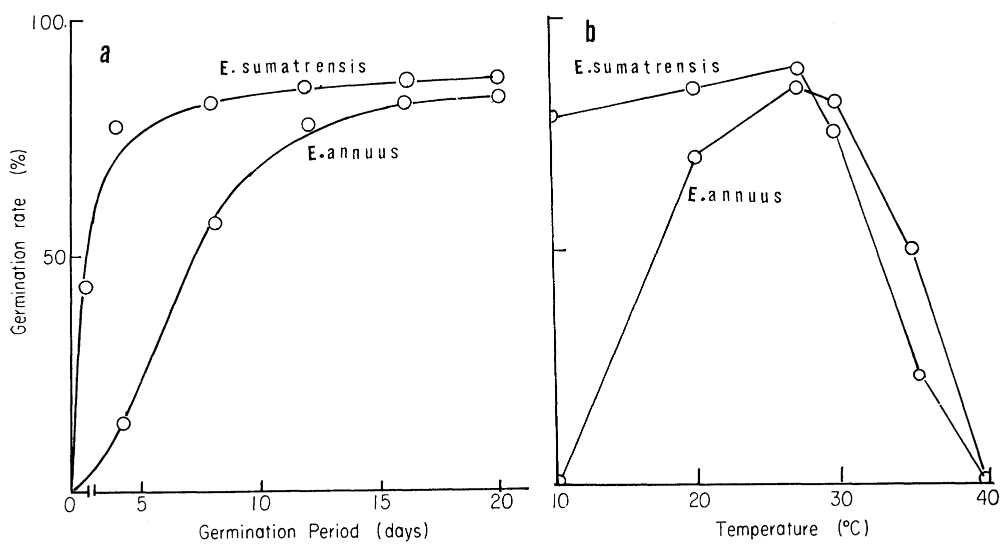

Fig. 6. Comparison of the germination behaviour of *Erigeron annuus* and *E. sumatrensis*, a, elapse in days untill a certain germination rate is obtained, and b, the temperature requirement for a good germination rate.

Discussion and Conclusion

The mechanism of secondary succession especially the establishment and alternation of early stage community may be elucidated by ecological analysis of the nature of species reaction, eco-physiological or biochemical, and the stratified or productive structure of such communities. Among these, studies on the autecology and the interaction of life-forms of dominant or common species in each stage of the secondary succession are not sufficient till today. According to Rice (1964[14]), the rate of plant succession on abandoned fields is due in part to the production of substances inhibitory to nitrogen-fixing or nitrifying bacteria by the pioneer species, such as *Aristida oliganta*, *Ambrosia elatior*, *Bromus japonica*, *Digitaria sanguinalis*, etc. Such an allelopathic or biochemical analysis is important to elucidate the mechanism of succession. As another way to analyse the mechanism of the alternation to early stages of the secondary succession, the authors are applying an eco-physiological and autecological analysis, especially on the germination behaviour of pioneer species. The seed weight of important pioneer species is shown in Fig. 1. The rank of the seed weight is as follows: *Ambrosia elatior*, *Steria lutescens*, *Rumex japonicus*, *R. congromeratus*, and *Digitaria adscendens*. The seeds of *Chenopodium album*, *Oenothera muricata*, and *Amaranthus retroflexus* are lighter than those. Namely the species of the pioneer community of the first stage established on a disturbed bare ground are greater in the seed weight than the species of the second stage community. It seems to be different from the conclusion that Salisbury (1942)[20] and Numata (1961)[6] discussed about the relationship between species appeared in seral stages and their seed weight. The general tendency is, in fact, the same as their conclusion, however some pioneer species especially of the first stage of secondary succession have somewhat larger or heavier seeds than any other species prevalent in the second year. Somewhat heavier seeds as such are favourable for germination and initial growth under severe conditions in a bare ground. They can grow in bad conditions as abrupt change of the microhabitat, i.e. dificiency of soil water content in summer, flying of surface soil in windy season, etc. Our attention goes to these small seeds as *Erigeron annuus* and *E. sumatrensis*, because they hardly establish pure stands in a bare ground at first. Numata *et al.* (1964)[11] already reported that the seed population of *Ambrosia elatior*, *Setaria viridis*, *Chenopodium album*, *Rumex japonicus*, *Cerastium viscosum*, *Erigeron annuus*, *Oenothera muricata* and *Capsella Bursa-pastoris* was buried in the field soil abundantly, however among these only the seeds of *Ambrosia* and *Setaria* can germinate and grow dominantly to make the first stage pioneer communities. In contrast with these seeds, the *Chenopodium* and *Oenothera* seeds are too small to grow vigorous seedling under such severe habitats as the abrupt alternation of dry and wet conditions in the surface soil and the flying of soil particles. Based on these results, the characters of germination of these seeds are discussed as related to the mechanism of succession. The common character of germination of pioneer species of the first stage community mentioned above is the slow progress of after-ripening and the strong accerelation to germination by the cold-treatment of 0°–3° or natural temperature condition in winter in the middle of Japan. On the contrary, *Erigeron annuus* and *E. sumatrensis* show a high germination rate immediately after harvesting and are never affected by the pre-treatment as stratification or burying-in-soil treatment in winter in the middle of Japan. The test of accerelation by these pre-treatments can not be directly applied to the explanation of the seed germination in the field. It is undoubtful if the rapid appearance of seedlings of *Ambrosia* in early spring prior to other species to establish a pioneer community is only due to the effect of the low temperature in winter for germination of the *Ambrosia* seeds. If the soil surface is disturbed in late spring or early summer or denuded after the germination of the *Ambrosia* seeds, the *Setaria* community will grow in the same stand (Numata et al. 1954[4]). Based upon the results mentioned above, we may say on the mechanism of establishment and development of plant communities in early stages of the secondary succession in the middle of Japan as follows: the important characters necessary for pioneer species of the first year stage are 1) having heavier seed weight than other common species in the second year stage and a great torelance of seedlings to unfavourable conditions on the bare ground, 2) benefitial effects or no inhibition at least by low temperatures in winter to accerelate the germination, 3) volleying in germination of the seed population by rather low temperatures, particularly, in early spring, and 4) the light requirement for germination being not necessary.

The germination of the *Chenopodium* and *Capsella* seeds is accerelated by the low temperature treatment and the burying-in-soil treatment in winter, but they hardly appear in the earliest stage of the secondary succession as the first year pioneer species, because the seeds are too small to make strong seedlings against severe conditions of a bare ground. In addition to these factors, the productivity of seeds, the dispersing capacity and the seed longevity must be examined later. *Erigeron annuus*, *E. sumatrensis* and *Oenothera muricata* which surpass the pioneers of the first year stage and dominate in the following stage of succession have very small and light seeds and distribute in the first year communities already grown. Further, they are characterized by high germination rates even in young after-ripening ages in a grown community and by the overwintering as the rosette form. They have all the so-called partial rosette form in the growth form classification. Thus the very diversity of the mode of life of species will be most important for advancing plant succession.

According to the general principle mentioned above, the mechanism of secondary succession in early stages in the middle of Japan is explained concretely as follows: the seeds of *Ambrosia elatior* and *Setaria lutescens*, which overwinter in the soil without germination from last autumn germinate, grow and establish a pioneer community exclusively under severe conditions in a bare ground. With establishment of such a community as the first year stage, environmental conditions of a denued ground change better for small seedlings of other species such as *Erigeron annuus* and *E. sumatrensis* which are able to grow under the reaction in an initial community. Under these conditions, *E. annuus* and *E. sumatrensis* grow and overwinter as rosette, and dominate in the second year stage surpassing *A. elatior* and *S. lutescens*. Thus the alternation of seral stages from the *A. elatior* community to the *E. annuus* is completed.

Literatures

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摘　　要

林　一六*・沼田　真**: 二次遷移初期に出現する種の種生態 I.

1) 遷移のメカニズムを解明するために，二次遷移初期の群落を構成する主要な種の種生態的検討をこころみた．そのためには，まずわが国中部における二次遷移初期群落の構成種14種を選んで，種子とその発芽の特性を調べた．さらに発芽試験のさいにみられる諸問題を整理し，生態学的問題点を指摘した．

2) 実験によると，二次遷移の出発点（裸地化の第1年度）の群落を構成する第一次先駆種は，種子重量が，比較的重く，発芽については後熟の進行がおそく，低温による前処理がいちじるしく促進的にきくことが明らかになった．ところが第2年度に優占する第二次先駆種というべきヒメジョオン，オオアレチノギクなどは，短い後熟期間でも常に高い発芽率を示し，低温処理，埋土処理の効果がなかった．

3) 第一次先駆種の中でも，とくにブタクサ種子では，低温処理は種子集団の発芽に一斉性を与え，より長い処理期間は低温領域の発芽を促進した．

4) 以上の結果から，わが国中部の二次遷移の進行のメカニズムは次のように説明できる．すなわち，二次遷移の出発点である裸地の環境は，埋土種子集団の中から発芽するエノコログサ，ブタクサの芽生えに有利に作用する．その結果成立する上記の種の優占する群落はその環境形成作用（土壌水分条件の安定化，土砂の移動をおさえる働き，初年度の先駆群落の保護作用）によって次の遷移段階で優占するヒメジョオン，オオアレチノギクなどを群落内に生育させるようになる．夏から秋にかけて発芽したそれら第二次先駆種はロゼット型で越冬し，翌春発芽態勢にあるブタクサなどを抑えて生育し，ブタクサ群落など初年度の群落からヒメジョオン群落など第2年度の群落へ遷移が進行する．(*東京教育大学菅平高原生物実験所・**千葉大学文理学部生物学教室)