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Ecology of Pioneer Species of Early Stages in Secondary Succession II. The Seed Production*

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Abstract

The life cycles of important species in early stages of the secondary succession are compared by the arthors to account the cause of replacement of species in the course of succession.

The present paper deals with the seed production of dominant species such as *Polygonum persicaria*, *Erigeron annuus*, *E. canadensis*, *Oenothera parviflora* and *Chenopodium album*, in the old field succession in central Japan. The plant height (H) and the diameter of stem at the base (D_o) are measured, and the number of seed grains (N_s) is counted. Furthermore the relationship between the seed production and quantities of plant bodies are examined. The equations to express the correlation of the seed production with the weight or volume estimated from D_o and H are as follows: *P. persicaria*: $\log N_s = 2.843 \log D_o + 4.061$, *E. annuus*: $\log N_s = 1.171 \log D_o + 4.948$, *E. canadensis*: $\log N_s = 2.676 \log D_o + 2.997$, *Oe. parviflora*: $\log N_s = 2.402 \log D_o + 4.770$, and *Ch. album*: $\log N_s = 3.944 \log D_o + 4.778$. Using these equations the seed production/$50 \times 50\ cm^2$ is estimated for *E. annuus* and *Ch. album*. The status of the species in the subseral community is discussed in relation to the seed production.

Introduction

The mechanism of plant succession may be explained by a comparative study on various phases of the life-cycle of dominant species as shown in our previous paper on the autecological study of pioneer species at early stages in the secondary succession (Hayashi and Numata, 1967[1]). The germination behaviour of pioneer species in central Japan was compared there. The present paper deals with the seed production of pioneer species from the similar viewpoint to clarify the mechanism of the secondary succession (Salisbury, 1942[2]; Newman, 1964[3], 1965[4]; Myerscough and Whitehead, 1966[5]; Welch, 1966[6]). The authors (Numata, Aoki and Hayashi, 1964[7]) formerly presented the concepts of GSP and SSP regarding the total number of buried seeds of a time. That is, the total number of buried seeds per unit area at a time is called the "gross buried seed population" (GSP) and the total number of seeds produced in one growing season of a seral stage per unit area is the "seral seed production" (SSP). A phenomenal SSP of the *Ambrosia* stage established in the first year after the denudation is about $16{,}500/1\ m^2 \times 1\ cm$ surface soil. The "income and outgo" of seeds in a plant community is like the energy flow or the

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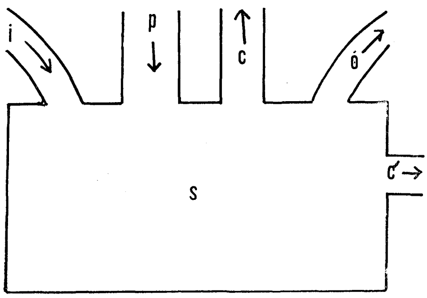

Fig. 1. The seed population dynamics of a plant community. p: production of seeds (SSP) by a community per unit area of soil surface in one growing season, c and c': consumption of seeds by germination and decay, grazing by animals, etc. per unit area in one growing season, i and o: invasion of seeds into the community from outside and outgo of seeds from the community to outside by various methods of dispersal per unit area in one growing season, s: storage of buried seeds in the soil under the community per unit volume at a time.

nutrient circulation in an ecosystem. GSP is a kind of "standing crop" of seeds which represents the underground storage of seeds. Here Numata's model on the income and outgo of seeds is shown in Fig. 1. The authors wish to complete the balance sheet of seed population as shown in Fig. 1 and to elucidate a factor affecting such seed population dynamics. In this paper the autors firstly tried to estimate the seed production of respective species.

Material and Methods

The species examined in this experiment are *Polygonum persicaria*, *Erigeron annuus*, *E. canadensis*, *Oenothera parviflora* and *Chenopodium album*. The seeds of these species were collected in Sugadaira, Nagano Prefecture, central Japan. These seeds were sampled from mature individuals of various sizes of

Table 1. The floristic composition of the communities dominated by *Polygonum persicaria* and *Erigeron canadensis*. The dominance is indicated by the three-factor summed dominance ratio.

Polygonum stand		*Erigeron* stand	
Species	SDR_3	Species	SDR_3
Polygonum persicaria	100.0	*Erigeron canadensis*	100.0
Elsholtzia ciliata	70.0	*E. annuus*	88.9
Chenopodium album	60.2	*Dactylis glomerata*	58.1
Erigeron annuus	37.7	*Rumex Acetosella*	48.6
Gramineae sp.	36.7	*Erigeron* sp. (rosette)	40.3
Erigeron canadensis	35.6	*Elsholtzia ciliata*	31.8
Stellaria media	30.3	*Trifolium repens*	27.2
Artemisia princeps	28.2	*Agropyron Kamoji*	16.4
Oenothera parviflora (rosette)	27.6	*Artemisia princeps*	13.0
Commelina communis	18.3	*Oenothera parviflora*	12.8
Poa annua	3.6	*Phleum pratense*	12.6
Achillea sibirica	3.6	*Setaria viridis*	10.5
Panicum Crus-galii	3.6	*Cerastium caespitosum* var. *ianthes*	10.4
Stellaria sp.	3.5	*Digitaria violascens*	8.3
Potentilla Freyniana	3.5	Gramineae sp.	7.3
Digitaria violascens	3.5	*Polygonum persicaria*	4.1
		Commelina communis	3.6
		Moehringia lateriflora	3.4

the dominant species in the communities. The floristic composition of the communities dominated by *Polygonum persicaria* and *Erigeron canadensis* is shown in Table 1. Mature plants of these species were collected before the falling of seeds, and the plant height (H), the diameter of stem at the base (D_o), and the number of seed grains produced (N_s) were measured. The extremely great number of small grains was estimated by the number of flowers per head and the number of seed grains per flower. The weight of seeds (100 grains for each species) was measured after oven-drying at 85°. Based on the measurement mentioned above, the relationships between N_s, the plant-body characters and D_o^2H were examined (cf. Shimizu, 1959[8]; Ohga and Numata, 1965[9]).

Results

Polygonum persicaria. This is one of the commonest farmland weeds and sometimes a pioneer species of secondary succession in Sugadaira.* It is a therophyte (summer annual) lacking any particular adaptation for wind dispersal. The germination rate increases by the low temperature treatment at 0–3° prior to the incubation for germination. Among the individuals sampled in a pioneer community. the plants of 1 m and 0.3 m in height, and 1.33 cm and 0.24 cm in diameter produced 10,370 and 185 seed grains respectively (Table 2). The general relationships of H, D_o, D_o^2H and N_s of various individuals were examined and are shown in Fig. 2 and Fig. 3. These are formulated as $N=aX^b$ ($X=D_o$, H or D_o^2H), similar to the formula of relative growth. Ohga and Numata (1965)[9] recognized the same relation between D_o (cm) and weight of trunk W_t (g) or weight of branches W_b (g) or weight of

Table 2. The seed production of five species of a pioneer community in secondary succession.

Species	Dry weight of 100 seed grains (mg)	Height of plants (m)	Diameter of stems (cm)	Seed production per plant (no. of grains)
Polygonum persicaria	131.4	1.00 0.75 0.32	1.33 0.82 0.24	10,370 5,002 185
Erigeron annuns	2.5	1.17 0.85 0.40	0.80 0.30 0.20	47,576 17,841 5,321
E. canadensis	3.6	1.65 0.80 0.28	0.89 0.29 0.14	153,110 17,710 4,480
Oenothera parviflora	40.4	1.39 0.66 0.35	1.60 0.41 0.25	81,200 4,930 1,015
Chenopodium album	46.0	2.15 1.36 0.88	1.26 0.52 0.27	52,240 7,426 301

* *Polygonum persicaria* dominated also in Chiba Prefecture in the first year stand after the denudation, where *Ambrosia artemisiifolia* (synonyms: *A. elatior* or *A. artemisiifolia* var. *elatior*) did not invade yet.

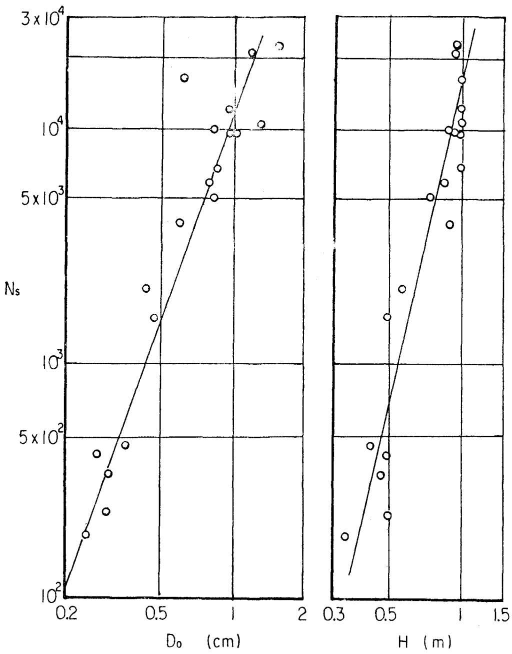

Fig. 2. Relations between the number of seed grains (N_s) and the diameter of stem at the base (D_o) (left) and plant height (H) (right) in *P. persicaria*.

leaves W_1 (g). Here we have equations as follows:

$$\log N_s = 2.843 \log D_o + 4.061 \quad \ldots\ldots (1)$$
$$\log N_s = 4.507 \log H + 4.164 \quad \ldots\ldots (2)$$
$$\log N_s = 1.053 \log D_o^2 H + 1.981 \quad \ldots\ldots (3)$$

Here the correlation coefficient between the number of seed grains and other characteristics of plant body is calculated as shown in Table 3. The value of the correlation coefficient varies with the portions related, but the correlation between the diameter of stem and the seed production seems to be highest in general.

Erigeron annuus. This species is as important as *E. canadensis* in early stages of the secondary succession in Sugadaira*. The seed has an equipment for wind dispersal and the seed weight is about 0.025 mg in dry weight. The germination rate of seeds is accerelated even by a low light intensity. The number of seeds per plant is 47,576

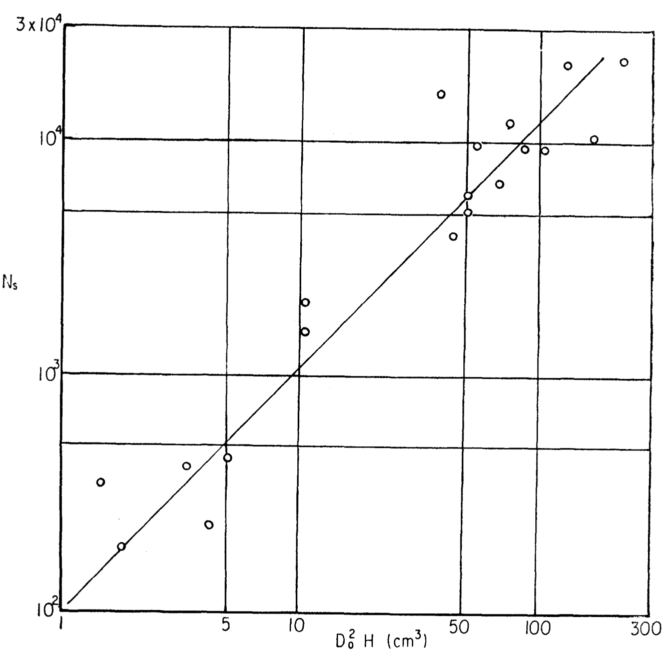

Fig. 3. Relation between N_s and D_o^2H in *P. persicaria*.

* Some species of *Erigeron* were introduced into Japan about 100 years ago and are widely distributed all over the country as pioneer species of secondary succession.

Table 3. The correlation coefficients of the number of seed grains produced to the characteristics of plant bodies of five pioneer species.

Species	N_s-H	N_s-D_o	N_s-D_o^2H
Polygonum persicaria	0.79	0.86	0.83
Erigeron annuus	0.87	0.93	0.90
E. canadensis	0.79	0.98	0.91
Oenothera parviflora	0.92	0.94	0.97
Chenopodium album	0.83	0.92	0.34

and 5,321 on the individuals of $H=1.17$ m, $D_o=0.80$ cm and of $H=0.4$ m, $D_o=0.20$ cm respectively. Relations of the seed production (N_s) to D_o, H and D_o^2H are shown in Figs. 4, 5 and fit to the equations as follows:

$\log N_s=1.171 \log D_o+4.948$ ....(4)
$\log N_s=3.661 \log H+4.491$ ......(5)
$\log N_s=0.587 \log D_o^2H+3.580$ ..(6)

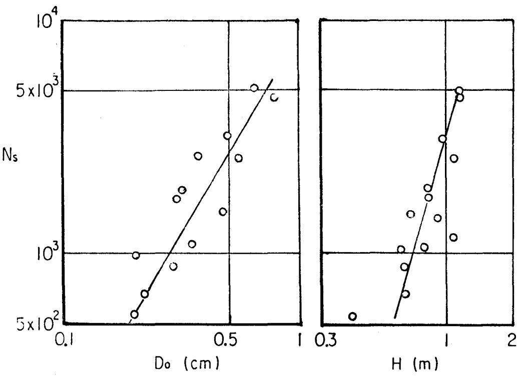

Fig. 4. Relations between N_s and D_o (left) and H (right) in *E. annuus*.

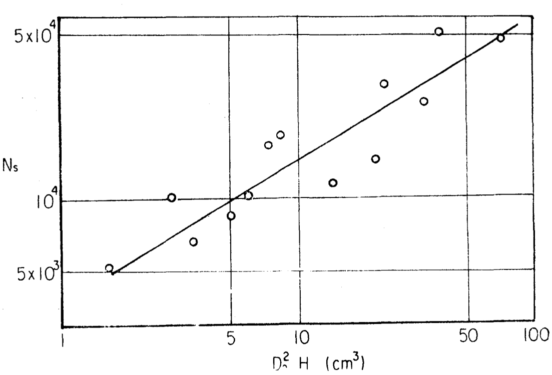

Fig. 5. Relation between N_s and D_o^2H in *E. annuus*.

E. canadensis. This species is an anemochore with the seed 0.036 mg in dry weight. The samples were collected inside and outside the second-year pioneer communty. The seed production inside the community is 152,110 and 4,480 on the plants of 1.65 cm (H), 0.89 cm (D_o) and 0.28 m (H), 0.14 cm (D_o) respectively. The relations of N_s to D_o, H and D_o^2H are shown in Figs. 6, 7 and fit to the equations as follows:

$\log N_s=2.676 \log D_o+2.997$ ......(7)
$\log N_s=2.916 \log H+4.593$ ......(8)
$\log N_s=0.943 \log D_o^2H+3.472$....(9)
$\log N_s=0.671 \log D_o^2H+3.921$....(9′)

(9′) is derived from the linear relation indicated by the solid circles in Fig. 6 and it represents the former relation of the individuals outside the community. It is clear from Fig. 6 that these individuals seem to produce the larger number of seeds than the individuals inside the community. In case of 60 cm or shorter in height the linear relations of N_s to D_o^2H and N_s to D_o in *E. canadensis* break at about 40 and 0.5 cm respectively.

As shown in Table 3, the correlation between the diameter of stem of plants and the seed production is great. These two species *E. annuus* and *E. canadensis*

Appendix Table. The crude data of the seed production of five species.

Polygonum persicaria			*Oenothera parviflora*			*Eirgeron canadensis*			H	D_o	N_s	*Chenopodium album*		
						(inside of community)			39	2.0	13.0	H	D_o	N_s
H	D_o	N_s	H	D_o	N_s	H	D_o	N_s*	42	1.9	10.1	215	12.6	52240
96	15.2	22385	133	14.8	92800	160	8.4	162.0	45	1.6	4.1	189	9.3	17480
95	12.0	20740	139	16.0	81200	165	8.9	152.1	28	1.4	4.5	175	7.4	17152
100	6.3	16025	123	15.3	63220	123	5.1	89.5	*Erigeron annuus*			153	6.6	16640
100	8.7	12078	109	11.2	49880	123	5.0	77.0	114	6.5	50080	197	8.6	12320
100	13.3	10370	98	7.1	30450	133	5.3	77.0	117	8.0	47576	136	5.2	7424
90	8.3	9943	97	9.4	30100	98	4.9	50.3	97	5.0	31613	146	5.1	6144
95	9.7	9455	94	9.3	23780	90	3.6	31.1	110	5.6	25353	102	3.1	857
100	10.3	9455	87	6.8	12470	80	2.9	17.7	85	3.2	19093	97	3.4	731
100	8.3	6832	83	6.9	11020	78	2.7	13.9	85	3.0	17841	105	3.0	656
83	7.9	5978	83	6.6	7540	66	2.4	13.7	94	4.8	14711	93	2.5	475
75	8.2	5002	68	4.1	4930	59	1.8	5.7	110	3.5	11216	88	2.7	301
90	7.0	3965	57	4.1	2900	53	1.7	4.1	81	2.8	10955	65	2.1	123
58	4.3	2074	55	3.7	2900	(outside of community)			67	2.1	10329			
50	4.6	1525	49	3.4	1595	94	4.4	63.8	68	2.8	8764			
42	3.5	448	45	2.6	1140	65	4.3	45.0	68	2.3	6886			
50	2.7	414	42	3.0	1450	59	2.7	21.8	40	2.0	5321			
48	3.0	340	35	2.5	1015	60	2.8	21.3						
51	2.9	250				54	2.6	21.0						
32	2.4	185				70	2.7	14.8						

* a unit: thousand

pass through winter as the rosette form and their dominant growth is often observed in the second year stage following the stage of the first year in the vicinity of Sugadaira, central Japan as well as in other places in Japan (Numata, 1956[10]; Numata and Suzuki, 1958[11]).

Oenothera parviflora. This is a winter annual. The weight of a seed grain is 0.40 mg in dry weight. The disseminule form belongs to D_1 in the Numata's disseminule classification. The plants of 1.39 m (H), 1.60 cm (D_o) and 0.88 m (H), 0.25 cm (D_o) produce 81,200 and 1,105 seeds respectively. The same relations as the former species are shown in Figs. 8, 9 and fit to the equations as follows:

$$\log N_s = 2.402 \log D_o + 4.770 \quad \text{..(10)}$$
$$\log N_s = 3.863 \log H + 4.505 \quad \text{..(11)}$$
$$\log N_s = 0.878 \log D_o^2H + 2.655 \quad \text{(12)}$$

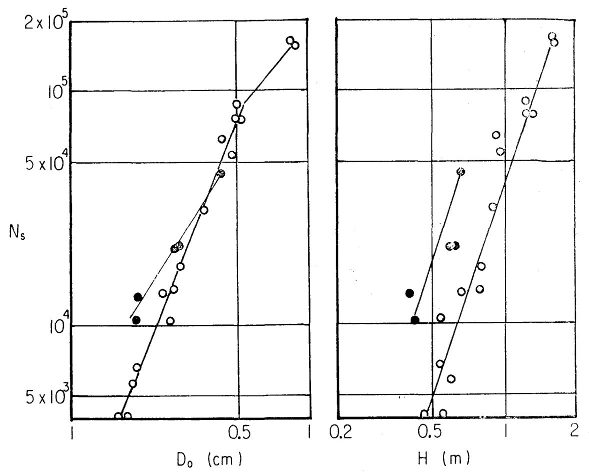

Fig. 6. Relations between N_s and D_o (left) and H (right) in *E. canadensis*. The solid circles indicate the plants growing outside the community.

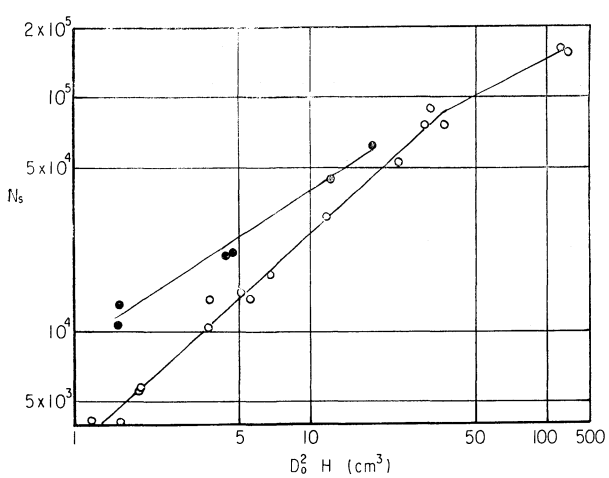

Fig. 7. Relation between N_s and D_o^2H in *E. canadensis*. The solid circles indicate the plants growing outside the community.

Chenopodium album. This is one of the arable weeds. The seed has no equipment for the dispersal by wind. The enormous number of the *Chenopodium* seeds is usually buried in the soil of early stages of secondary succession. The number of seed grains per plant is 52,240 and 301 on the plants of 2.15 m (H), 1.26 cm (D_o) and 0.88 m (H), 0.27 cm (D_o) respectively. The same relations as mentioned above are shown in Figs. 10, 11 and fit to the equations as follows:

$$\log N_s = 3.944 \log D_o + 4.778 \quad \text{..(13)}$$
$$\log N_s = 5.345 \log H + 2.903 \quad \text{..(14)}$$
$$\log N_s = 1.277 \log D_o^2H + 1.522 \quad \text{(15)}$$

The seed production per individual in various sizes of each species was examined as above, but few data of the seed production have been obtained from certain communities. The height of plant and the diameter of stem at the base were measured for all plants in the quadrats of 50×50 cm² in the communities dominated by *Erigeron annuus* and *Chenopodium album*. The investigation was carried out at the time of mature stage of plants. 58 individuals grew in a quadrat of $50 \times 50\ cm^2$ in the *Erigeron* stand. The histogram of plant height is shown in Fig. 12. In general, the distribution of individual weight is of L-shape while that of height is of J-shape (Koyama and Kira, 1956[12]). The situation is not the same in *Ambrosia artemisiifolia*. That is, the distribution type of the weight of *A. artemisiifolia* is symmetrical in the seedling stage, but later appears a J-shape with two modes at the upper and the lower layers (Numata and Yamai, 1955[18]). The distribution type seen in Fig. 12 is not so clear

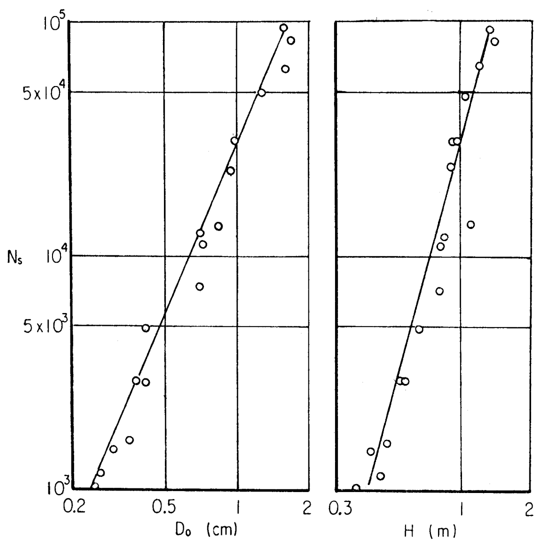

Fig 8. Relations between N_s and D_o (left) and H (right) in *Oe. parviflora*.

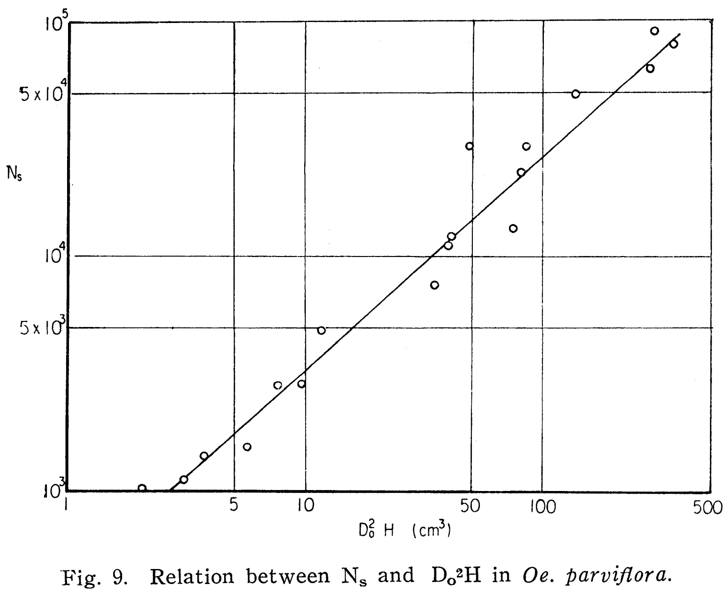

Fig. 9. Relation between N_s and D_o^2H in *Oe. parviflora*.

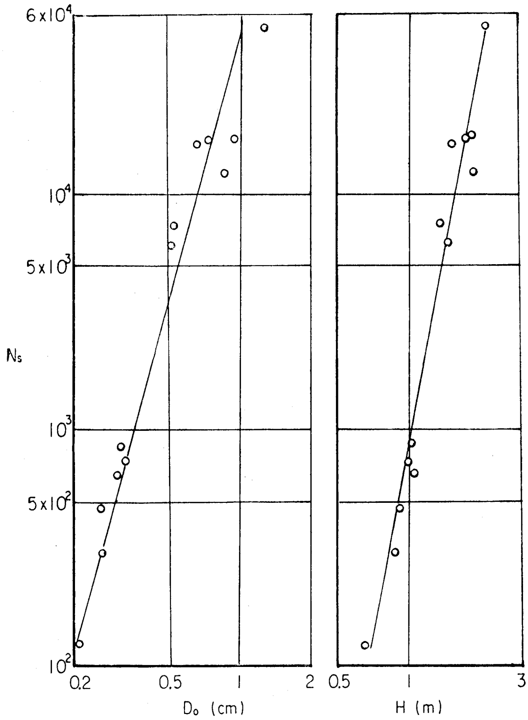

Fig. 10. Relations between N_s and D_0 (left) and H (right) in *Ch. album.*

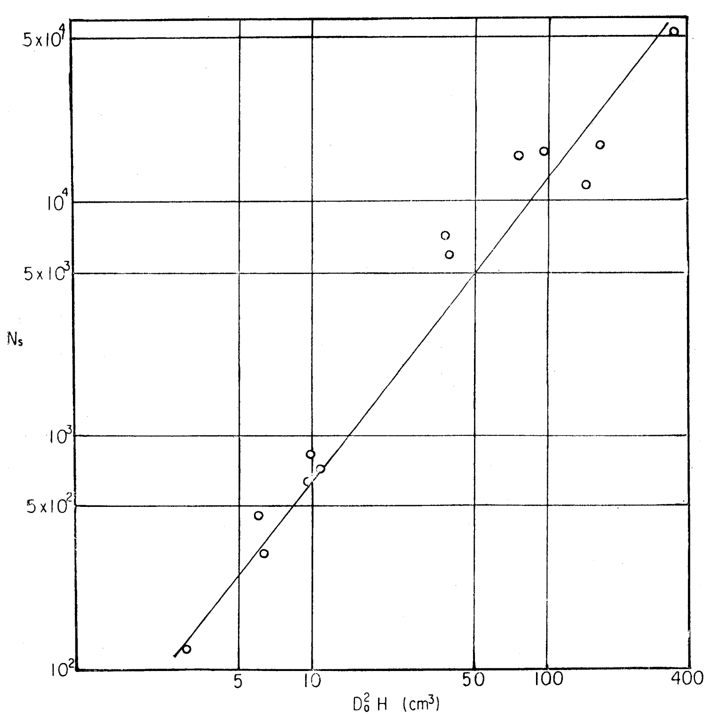

Fig. 11. Relation between N_s and $D_0{}^2H$ in *Ch. album.*

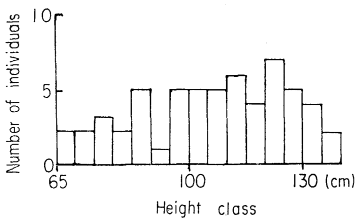

Fig. 12. The histogram of plant height of *E. annuus* in the quadrat of 50×50 cm^2. The individual density is $58/50 \times 50$ cm^2.

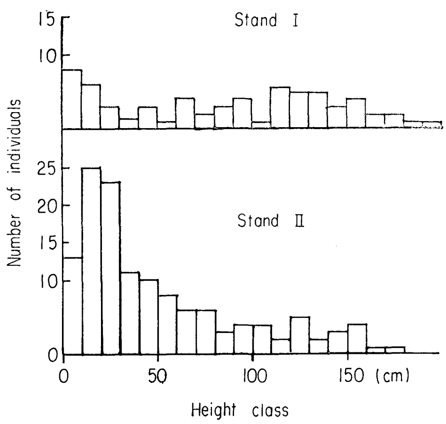

Fig. 13. The histogram of plant height of *Ch. album* in the quadrat of 50×50 cm^2. The individual density is 66 and $131/50 \times 50$ cm^2 in the stand I and II respectively.

but seems to be rather J-shaped. In the *Chenopodium* stand, two quadrats of the same size, in which 131 and 66 individuals of *Chenopodium* grew, were sampled. The histograms of plant height in both stands are shown in Fig. 13. They, particularly in the stand II, are characterized by the L-shape like the distribution of individual weight. The difference between these two histograms suggests that though the stands seem apparently homogeneous in the physiognomy, the height distribution of these stands actually differs as follows: in the stand II, several tall individuals occupy the upper layer of the community and a considerably large number of middle or low individuals constitutes the lower layer like the *Ambrosia* community (Numata and Yamai, 1955[13]), while in the stand I many tall individuals occupy the upper layer densely and therefore only a few individuals grow in the lower layer. As regards the total seed production of the stand, the latter produces larger number of seeds than the former.

Based on the measurement of the plant height and diameter of stem, the total number of seeds/50×50 cm^2 of *E. annuus* and *Ch. album* is estimated using the equations (9) and (10). 58 individuals of *E. annuus*/50×50 cm^2 may produce about 1,200,000 seed grains and 66 and 131 individuals of *Ch. album*/50×50 cm^2 may produce about 224,000 and 105,000 seed grains respectively.

Discussion and Conclusion

The relationship of the seed production to the characters of the plant body such as the height (H), the weight estimated by D_0^2H, etc. is examined as above, and the correlation between them differs according to various growth forms of species. For example, in the clump form, branching at the basal part of the stem, such as *Polygonum persicaria*, the seed production highly correlates with the diameter of stem at the base, while in the erect from as *Oenothera parviflora*, the weight correlates better with the seed production. The species examined above are all annuals or biennials appearing in early stages of the secondary succession and for these species the seed production plays an essential role in the completion of their life-cycle. The seed production of perennials, however, does not always play the same role in the life-cycle as that of annuals. Therefore the application of the relations mentioned above must be restricted to annuals and biennials in which the seed stage makes an essential part in the life-eycle.

Among five species mentioned above, *Polygonum persicaria* may be one of the pioneer species of the first year stand of an old field succession. This species has heavy seeds lacking any equipment for dispersal and produces fewer number of seed than the second year pioneer, *Erigeron annuns*, etc. On the contrary, *E. annuus* and *E. canadensis* produce enormous number of small seeds belonging to the anemochore (D_1). *Oenothera parviflora* differs from the two species of *Erigeron* in having heavier seeds and having no equipment for wind dispersal. *Chenopodium album* as well as *Polygonum persicaria* have not any equipment for seed dispersal and the life-form of overwintering rosette, but they are considered to be disseminated by birds (D_2) (Ridley, 1930[14]). *Ambrosia artemsiifolia** reported in the previous paper is also the bird-dispersal type (Ridley, 1930[14]). Therefore the bird-dispersal type (D_2) seems to be the charcteristics of the first year pioneer species in the old field succession, and the wind-dispersal type of small seed like *Erigeron* may be the characteristics of the second year pioneer species.

The germination behaviour of the seed population produced by a mother plant of *Chenopodium* is characterized by a gradual increase of germination rate, so a rapid occurrence of most seedlings is not observed under field conditions. The comparative autecology of such species concerning the seed production and the germination behaviour is necessary for clarifying the mechanism of plant succession. Furthermore the behaviour and growth of the seedlings and young plants must be studied from the viewpoint of experimental sociology as done by Knapp (1954[15]). The effect of interspecific competition on the seed production in wild plants was discussed by Salisbury (1942[2]), and that of intervarietal competition in crops by Yamada (1955[11]). This effect of competition occurred in our data, too, as effect of density. However, the full information on this problem will be described in a later paper.

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* Dr. Willard W. Payne of the University of Illinois, a taxonomist of *Ambrosia*, told one of the authors, Numata during his stay at Urbana in Feb., 1967, about the experiment of Alaw I. Gebben on the distributional ecology of *Ambrosia*. According to his experiment, the *Ambrosia* seeds germinate from the droppings of English sparrow introduced in U. S. A.

摘 要

林 一六*・沼田 真**: 二次遷移初期に出現する種の種生態, II. 種子生産について

2次遷移における種の交代の理由を明らかにするために群落を構成する種の生活環の諸相を比較しているが,本報告では重要な先駆種の種子生産量を比較した.長野県菅平地方に優占する先駆種であるハルタデ,ヒメジョオン,ヒメムカシヨモギ,アレチマツヨイグサ,シロザの5種についていろいろな大きさの個体の草丈と根元の直径とを測り,その生産した種子数を数えた.さらにそのような植物の各部分の大きさと種子生産量との間の相関を検討した.その結果種子生産量をN_s,植物体の草丈H,根元の直径D_oとすると各種の各大きさの個体の種子生産量は次のように示される.ハルタデ: $\log N_s = 2.843 \log D_o + 4.061$,ヒメジョオン: $\log N_s = 1.171 \log D_o + 4.948$,ヒメムカシヨモギ: $\log N_s = 2.676 \log D_o + 2.997$,アレチマツヨイグサ: $\log N_s = 2.402 \log D_o + 4.770$,シロザ: $\log N_s = 3.944 \log D_o + 4.778$.この結果を用いてヒメジョオン・シロザの優占する群落中の種子生産量を推定した.前者では個体密度58本/50×50 cm^2で約120万粒,後者では個体密度66/50×50 cm^2, 131/50×50 cm^2でそれぞれ約22.4万,10.5万粒である.種子の重量からみると初年度に優占するブタクサ,ハルタデ,シロザなどは鳥によって運ばれる(D_2型)比較的大型の種子で,第2年度に優占するヒメジョオン,ヒメムカシヨモギなどは風によって運ばれる(D_1型)小型の種子であることは興味深い.種子生産量には種内および種間の競争がきくであろうが,その詳細は後報にゆずりたい.ここではまず2次遷移の初期に優占する種の種子生産とその意義が検討されたが,それを通して沼田ら(1964)が提案したGSP, SSPの概念をふくめ,ある群落における種子量の収支関係(Fig. 1)を明らかにしていきたい.(*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)