

ヨモギ属植物近縁2種(エゾヨモギとヤブヨモギ)の生活史に関する研究: 1.
北海道東部の人里における生態分布と個体群構造

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Shuichi NAKAYAMA*: Life History Studies of the Two Closely Related *Artemisia* Species,

A. montana PAMP. and *A. rubripes* NAKAI (Compositae)

1. Ecological Performance and Wild Population Structures in Ruderal Habitats of Eastern Hokkaido, Japan.

中山修一*: ヨモギ属植物近縁2種(エゾヨモギとヤブヨモギ)の生活史に関する研究
1. 北海道東部の人里における生態分布と個体群構造

Introduction

Critical comparative studies on the life history traits of closely related species or species complexes provide us with significant information concerning their adaptive as well as evolutionary status. Many recent studies of life history characteristics and evolution in plants have focussed on the patterns of energy allocation to various life activities, including growth and reproduction (MONSI, 1960; HARPER and OGDEN, 1970; KAWANO, 1975; 1985; KAWANO and NAGAI, 1975; 1986 in press; SOULE and WERNER, 1981; EVENSON, 1983-review).

In the present series of studies on the two species of the genus *Artemisia* belonging to section *Vulgares*, Compositae in Japan, i. e., *A. montana* PAMP. and *A. rubripes* NAKAI (KITAMURA, 1940), the present author has attempted to clarify, firstly, their biological features, secondly, the resource allocation patterns to reproduction in both natural and artificial experimental populations of these two *Artemisia* species, and thirdly, to shed light upon their evolutionary-ecological status. This paper, as one of this series, aims to describe the ecological distributions and population structures of these two species in eastern Hokkaido, and furthermore to clarify their ecological status in the ruderal or weedy plant communities and also in successional environments.

Materials and Methods

Two colonizing *Artemisia* species, i. e., *A. montana* and *A. rubripes*, were chosen for the present study. *A. montana* is a native species and

representative member of the weedy or ruderal communities in Hokkaido, northern Japan, whereas *A. rubripes* is regarded as an introduced species from continental China now expanding to ruderal habitats in southeastern Hokkaido, mainly Tokachi, Abashiri and Iburi Counties

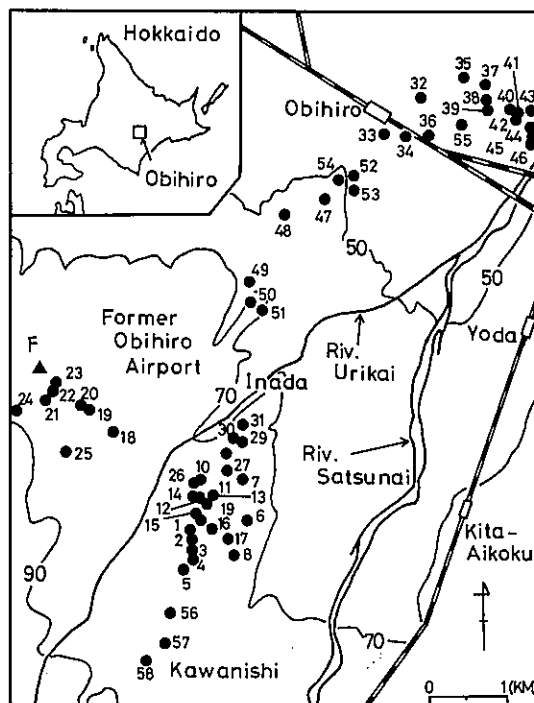


Fig. 1. Map showing the research sites in Obihiro City and its vicinity, Hokkaido Japan. Fifty eight stands (1-58) were surveyed for species composition associations and community structures. ▲ specifies the old field (stand F) where the population structures of two *Artemisia* species were surveyed.

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(NAKAYAMA, 1983). These two *Artemisia* species are now growing most abundantly on roadside and abandoned fields in southeastern Hokkaido, where human impacts are frequent, and both co-exist in the ruderal habitats of southeastern Hokkaido, especially in Obihiro City and its vicinity in Tokachi County.

Community structure and ecological performance of *Artemisia* species

Vegetation in artificial habitats such as trails, roadsides and old fields was surveyed at 58 stands in Obihiro City and its vicinity in Hokkaido, Japan (Fig. 1). Human impact at each stand was estimated based on visual signs of cutting, trampling, treading, and plowing. Research stands, covering a minimum of 30 m², were selected in the study area based on observed visual discontinuities in vegetation.

In September 1978, the coverage and plant height were examined for each component species

of the communities at all stands using five 1 × 1 m² quadrats. The cover degree was recorded according to the method of Braun-BLANQUET (1932). In order to classify the vegetation, the cluster analysis was conducted as follows : firstly, all species data on a species-stand matrix were prepared in the form of presence/absence. A matrix of Sørensen's inter-stand coefficient (Sørensen, 1948) was computed based on the above-mentioned reformed species-stand matrix. Secondly, clustering was done by the group-average method based on the inter-stand matrix (Greig-SMITH, 1957).

In each vegetation type which was defined by the cluster analysis, the frequencies and coverage values of *A. montana* and *A. rubripes* were compared with each other.

Population structures of two *Artemisa* species in an old field

In early July 1980, the size class structures of

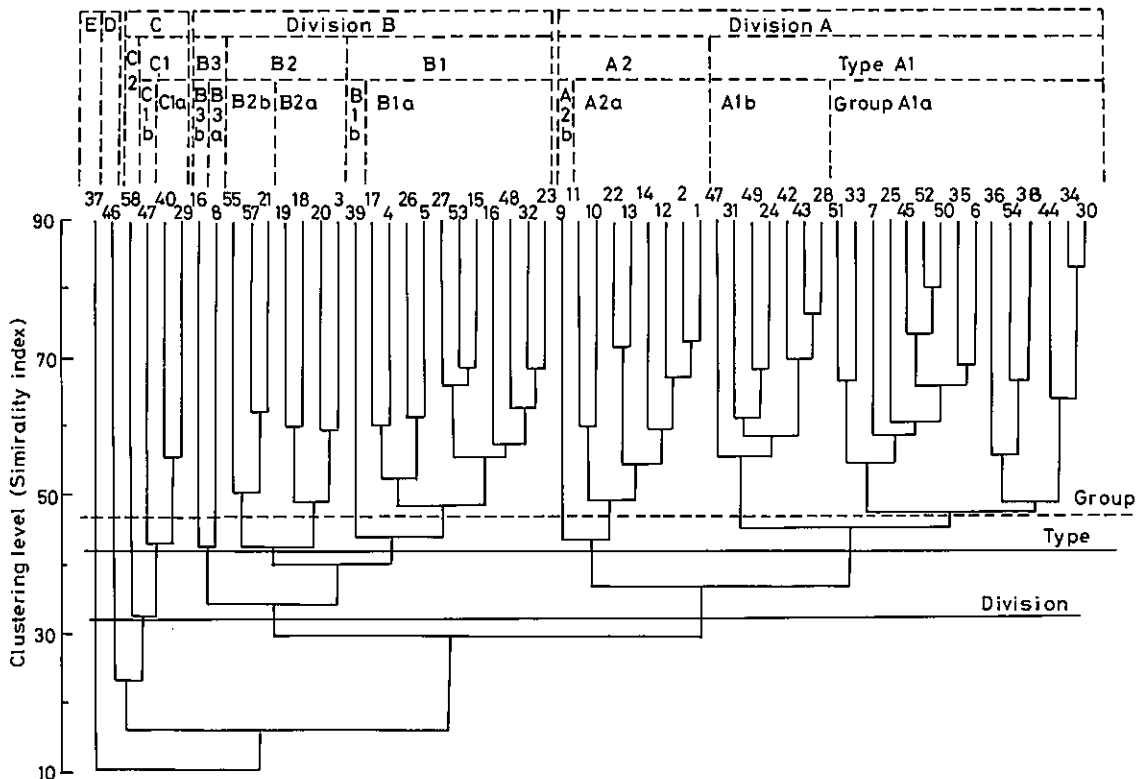


Fig. 2. The dendrogram illustrating different levels of similarity index as to species association in plant communities comprising *Artemisia* species in the ruderal habitats according to Sørensen's Inter-stand Coefficient (Sørensen, 1948).

populations of *Artemisia montana* and *A. rubripes* were investigated in two 5 × 10 m² plots (Plot A and B) which were established in the center of an 30 × 100 m² field (stand F) abandoned since 1976, near Obihiro City in Hokkaido. Previously, such crops as potato, soybean, and beet were cultivated in rotation in this old field.

In this site, the coverage and plant height of all species were first examined in five 1 × 1 m² quadrats. For the sampled individuals of *A. montana* and *A. rubripes*, the following characters were measured: diameter at the base of the stem (Do), shoot height (H), and shoot number. The individuals and ramets of the two

Artemisia species were mapped in Plot A. Sampled stems of both species were then brought back to the laboratory, and the relationships between stem biomass and $\sum_{i=1}^n (Do^2 \times H)$ were examined for both *Artemisia* species.

Results and Discussion

Community structure and ecological performance of the *Artemisia* species

(1) Cluster analysis: Figure 2 shows the cluster analysis dendrogram. At three different levels, groups can be separated by the group-average method. The first is a group of stands which can be separated at the 32.5 level of

Table 1. Frequency (F) and coverage value (CV) of the predominant species found in each vegetation type. Those with F less than II and CV less than 1000 throughout all six vegetation types, were not included in this Table.

Cluster group (Vegetation types)	A 1		A 2		B 1		B 2		B 3		C	
	Number of stands		9		12		7		2		4	
<i>Poa annua</i> L.	F	CV**	F	CV	F	CV	F	CV	F	CV	F	CV
<i>Polygonum aequale</i> LINDM	IV	1324
<i>Matricaria matricarioides</i> PORTER	III	239
<i>Sagina japonica</i> OHWI	III	104
<i>Chenopodium album</i> L.	V	631	IV	1973
<i>Digitaria violascens</i> LINK	IV	536	IV	697
<i>Echinochloa crus-galli</i> BREAUV. var. <i>crus-galli</i>	III	70	II	2
<i>Rorippa sylvestris</i> BESSER	III	115	II	194
<i>Polygonum longisetum</i> DE BRUYN	III	366	V	862	II	3	II	167
<i>Setaria faberi</i> HERRM.	II	296	IV	61	I	1
<i>Polygonum nepalense</i> MEISN.	II	47	III	446	I	1	I	82
<i>Erigeron canadensis</i> L.	III	162	III	113	II	3	I	2
<i>Elythria ciliata</i> HYLANDER	II	70	V	752	I	147	I	2	III	5	.	.
<i>Stellaria media</i> VILL.	III	150	IV	973	.	.	II	3	.	.	II	2
<i>Capsella bursa-pastoris</i> MEDIK.	.	.	III	43
<i>Rumex obtusifolius</i> L.	I	5	V	420
<i>Amaranthus patulus</i> BERTOLONI	I	1	III	113	I	71
<i>Rorippa islandica</i> BORBÁS	I	1	IV	641	.	.	I	2
<i>Polygonum lapathifolium</i> L.	I	1	III	60	I	1	I	2
<i>Sonchus brachyotus</i> DC.	I	1	IV	750	II	84	III	416
<i>Plantago asiatica</i> L.	V	705	I	56	V	310	I	2
<i>Taraxacum officinale</i> WEBER	V	628	II	4	IV	398	II	2
<i>Trifolium repens</i> L.	III	1193	IV	1030	III	524	IV	966
<i>Erigeron annuus</i> PERS.	III	93	IV	699	III	273	IV	966	III	250	.	.
<i>Setaria glauca</i> BEANV.	III	286	I	1	II	3	II	3
<i>Trifolium pratense</i> L.	III	206	II	57	IV	438	III	253
<i>Agrostis alba</i> L.	III	682	II	111	V	566	V	2964	.	.	II	438
<i>Oenothera biennis</i> L.	II	104	V	149	III	86	I	1
<i>Dactylis glomerata</i> L.	II	353	.	.	III	771	.	.	III	250	.	.
<i>Phleum pratense</i> L.	IV	346	.	.	V	2751	V	535	III	5	.	.
<i>Geranium thunbergii</i> SIEB. et ZNCC.	II	114	.	.	V	1212	II	7	V	750	.	.
<i>Agropyron repens</i> P. BEAUV.	III	342	IV	1779	III	813	III	1214	V	2125	II	2
<i>Poa pratensis</i> L.	IV	1240	.	.	V	3833	II	86	V	225	III	2625
<i>Artemisia rubripes</i> NAKAI	III	105	IV	170	V	688	V	1786	V	875	IV	302
<i>Artemisia montana</i> PAMP.	II	24	II	111	V	1647	V	1931	V	1925	IV	1817
<i>Breca setosa</i> KITAM.	III	168	III	394	.	.	IV	130
<i>Salix integra</i> THUNB.	I	1	III	144
<i>Equisetum arvense</i> L.	I	83	III	286
<i>Achillea millefolium</i> L.	III	144
<i>Helianthus tuberosus</i> L.	V	5000	.	.
<i>Sasa nipponica</i> MAKINO	I	188	II	537	.	.	III	1750
<i>Miscanthus sinensis</i> ANDERSS	I	1	.	.	I	1	III	1690

* F: I, 0-20%; II, 20-40%; III, 40-60%; IV, 60-80%; V, 80-100%.
 * * CV = (C/N) × 100; C, sum of the values of percentage cover degree in each vegetation type (5, 87.5%; 4, 62.5%; 3, 37.5%; 2, 12.5%; 1, 5%; +, 0.1%) and N, number of stands in each vegetation type.

clustering, called Divisions. The second is Types, which can be distinguished at the 42.5 clustering level. The third is Groups, which are separated at the 47.5 level of clustering.

In the present study, Types are used for distinguishing basic vegetation units. Nine types can be distinguished, but three types (Types C2, E

and D) are represented by a single stand (Fig. 2). Type C2 was included in Type C1, and was called Type C for convenience. Types E and D were excluded from the present analysis, since only single stands were recognized here.

(2) **Vegetation unit**: The following six vegetation types were distinguished.

Type A1: This vegetation type is found on trails or roadsides which are strongly disturbed by human trampling and agricultural machinery (Tables 2 and 3). The mean vegetation cover and height were ca. 68% and 32 cm, respectively, which were the lowest among all vegetation types. Otherwise, the diversity index in Type A1 was the highest of all the type (Table 4).

Type A1 is characterized by the presence of *Poa annua*, *Polygonum aequale*, *Matricaria matricarioides*, *Sagina japonica*, etc. and also by the predominant occurrence of *Plantago asiatica*, *Poa pratensis*, *Chenopodium album*, *Taraxacum officinale*, and *Trifolium repens* (Table 1).

Type A2: Most of the stands of this type occur in the old fields at the early stage of secondary succession. However, one stand of this type occurred on roadsides adjacent to the crop field, which was once subjected to heavy tractor disturbance (Tables 2 and 3). The mean proportion of annuals and biennials to the total number of species (Ab ratio) was highest in this vegetation type among all vegetation types, while the mean vegetation cover and height were the lowest, next to Type A1 (Table 4).

This type is characterized by species such as *Polygonum longisetum*, *Setaria faberi*, *Elsholtzia ciliata*, *Stellaria media*, *Capsella bursa-pastoris*, *Rorippa islandica*, *Amaranthus patulus*, *Polygonum lapathifolium*, *Rumex obtusifolius*, and

Table 2. Relationships between vegetation types and habitats. Figures specify the number of stands.

Vegetation types Habitats	A1	A2	B1	B2	B3	C
Trails	8	0	0	0	0	0
Roadsides	14	1	10	2	2	4
Abandoned grasslands	0	0	2	0	0	0
Abandoned fields	0	8	0	5	0	0
Total	22	9	12	7	2	4

Table 3. Relationships between vegetation types and human impacts given recently. Figures show the number of stands.

Vegetation types Criteria	A1	A2	B1	B2	B3	C
Number of stands	22	9	12	7	2	4
Trampling	18	0	1	0	0	0
Cutting and mowing	3	0	5	0	0	1
Plowing	4	9	0	0	0	0
No human impacts	0	0	6	7	2	3

Table 4. Vegetation structures in each vegetation type.

Vegetation types Criteria	A 1	A 2	B 1	B 2	B 3	C
Vegetation cover (%)	67.7±17.1	81.3±19.5	94.1±6.0	95.9±5.1	97.5	95.2±3.1
Vegetation height (cm)	31.5±24.1	60.4±55.6	70.2±35.3	89.9±29.0	161.2	104.0±53.5
Ab ratio* (%)	51.4±12.7	65.0±12.2	15.4±8.9	19.9±10.7	11.6	3.1±4.2
No. of species (No./5 m ²)	17.2±4.4	17.3±3.0	17.3±4.3	17.9±6.3	9.5	11.0±1.9
Simpson's Diversity Index	8.40±3.60	7.79±3.90	7.17±2.84	7.48±4.37	3.13	3.02±0.89

* Ab ratio indicates the proportion of annuals and biennials to the total number of species recorded.

Sonchus brachyotis. Furthermore, *Oenothera biennis*, *Erigeron annuus* and *Trifolium repens* were representative species which occurred frequently in this type (Table 1).

Type B1: Most of the stands of this vegetation type occur on roadsides which are subjected to mowing or cutting once or twice a year. However, two stands of this type were found also in the abandoned artificial grasslands (Tables 2 and 3).

There is no particular species group which is confined to and thus characterizes this vegetation type. Type B1 was composed of pasture grasses and forbs, i. e., *Agrostis alba*, *Phleum pratense*, *Poa pratensis*, *Dactylis glomerata*, *Trifolium pratense*, *T. repens* etc., and also weedy perennial herbs, i. e., *Plantago asiatica*, *Taraxacum officinale*, *Geranium thunbergii*, *Artemisia rubripes*, *A. montana*, etc. (Table 1).

Type B2: Most of the stands of this type occur in the old fields at the late stage of secondary succession. However, two stands of this type were found on roadsides adjacent to the crop fields or old fields, which were once subjected to heavy disturbance from human activities (Tables 2 and 3). *Trifolium repens*, *Erigeron annuus*, *Agrostis alba*, *Phleum pratense*, *Artemisia montana* and *A. rubripes* predominantly occur in this vegetation type also (Table 1).

Types B3 and C: The stands of these vegetation types occur on roadsides without recent human impacts (Tables 2 and 3). The mean diversity index, number of the species per stand, and Ab ratio of these types were much lower as compared with other vegetation types. Type B3 is characterized by the predominant occurrence of perennial plants such as *Helianthus tuberosus*, *Artemisia montana*, *A. rubripes*, *Agropyron repens*, *Poa pratensis*, etc., whereas in Type C, *Miscanthus sinensis*, *Sasa nipponica*, *Artemisia montana*, etc. are predominant (Table 1), and thus this vegetation type may be the more mature one.

(3) Ecological performance of the two *Artemisia* species: Table 5 shows the relative frequency, coverage value and RC ratio of *Artemisia montana* and *A. rubripes* in six vegetation types. The RC ratio was calculated as $100 \times (\text{coverage value})/(\text{relative frequency})$. This value can be regarded as an indicator of lateral expanding growth of the two *Artemisia* species.

The relative frequency and coverage value of the two *Artemisia* species were lower in Types A1 and A2 as compared with those of the other vegetation types, i. e., Types B1, B2, B3, and C. It is interesting to note here that the relative frequency and coverage value of *A. rubripes*, an introduced weedy species, were much higher than those of *A. montana*, a native ruderal species, in Types A1 and A2. This is probably due to a reproductive characteristic of *A. rubripes*, which increases its population size more rapidly by means of sexual reproduction than *A. montana*.

In Types B1, B2, B3, and C, the relative frequency and coverage value of *Artemisia montana* were 40.0 to 61.7 % and 1647 to 2104, respectively; whereas these indices of *A. rubripes* were markedly higher in Type B2 (relative frequency: 93.7 % and coverage value: 1786) as compared with those in Types B1, B3, and C (relative frequency: 50.0-53.3 % and coverage value: 302-875). Furthermore, it is apparent from Table 2 that Type B2 is characteristic of the old fields, while Types B1, B3, and C are limited to the roadsides. These differences in ecological performance of *A. rubripes* suggest that this species can establish a much larger population size in old fields than in roadsides.

Table 5. Relative frequency (RF), Coverage value (CV) and RC ratio of the two *Artemisia* species in each vegetation type.

Vegetation types	A1	A2	B1	B2	B3	C
Number of quadrat	110	45	60	35	10	20
Relative frequency						
<i>A. montana</i>	5.4	6.7	61.7	51.4	40.0	48.0
<i>A. rubripes</i>	14.6	28.9	53.3	94.3	50.0	52.0
Coverage value						
<i>A. montana</i>	24	111	1647	1931	1925	2104
<i>A. rubripes</i>	105	170	688	1786	875	302
RC ratio*						
<i>A. montana</i>	452	1657	2679	3757	4813	4383
<i>A. rubripes</i>	719	588	1291	1894	1750	581

* (RC ratio) = (CV/RF) × 100

The RC ratios of *Artemisia montana* were much higher than those of *A. rubripes* in the five vegetation types, except for Type A1. This result suggests that the lateral expanding growth of plants is more vigorous in *A. montana* than *A. rubripes* in the sites where no severe disturbance (i. e., trampling) occurs.

Population structures of two *Artemisia* species in an old field population

Table 6 shows the species composition of the sampling site in an old field in 1980. *Artemisia rubripes*, *Agropyron repens*, *Trifolium repens*, and *Artemisia montana* predominantly occurred in this site.

(1) **Size Classes:** In addition to the seedling stage, individuals of the two *Artemisia* species were empirically classified into 4 different size-classes based on the two characters (i. e., the number of stems per plant and absence and/or presence of lateral runners), as shown below:

Class 1: seedling;

Class 2: individuals with a single stem but no lateral runners;

Class 3: individuals with more than two stems but no lateral runners;

Table 6. Species composition of stand F.

Quadrat number (1 × 1 m ²)	1	2	3	4	5	CV
Vegetation cover (%)	40	90	60	80	80	
Number of species	11	11	10	8	9	
<i>Artemisia rubripes</i> NAKAI	2	3	2	3	1	3600
<i>Agropyron repens</i> P. BEAUV.	1	4	3	•	2	2350
<i>Trifolium repens</i> L.	1	3	1	•	4	2200
<i>Artemisia montana</i> PAMP.	1	•	3	4	1	2200
<i>Polygonum longisetum</i> De BRUYN	2	1	•	1	+	452
<i>Erigeron annuus</i> PERS.	2	+	•	1	+	452
<i>Elsholtzia ciliata</i> HYLANDER	1	+	•	1	•	202
<i>Potentilla fragarioides</i> L. var. <i>major</i>	•	•	+	2	•	252
<i>Oenothera biennis</i> L.	•	1	•	+	•	102
<i>Taraxacum officinale</i> WEBER	•	+	1	•	•	102
<i>Phleum pratense</i> L.	1	•	•	•	+	102
<i>Sonchus brachyotis</i> DC.	+	•	+	•	•	4
<i>Lythrum salicaria</i> L.	•	•	+	•	+	4
<i>Rorippa islandica</i> BORBÁS	+	•	•	+	•	4
<i>Rumex obtusifolius</i> L.	1	•	•	•	•	100
<i>Breca setosa</i> KITAM.	•	1	•	•	•	100
<i>Juncus tenuis</i> WILLD.	•	•	1	•	•	100
<i>Agrostis alba</i> L.	•	•	1	•	•	100
<i>Barbarea orthoceras</i> LEDEB.	•	+	•	•	•	2
<i>Chenopodium album</i> L.	•	+	•	•	•	2
<i>Achillea millefolium</i> L.	•	•	•	•	+	2

Table 7. Size class structures and mean shoot number per plant of the populations of two *Artemisia* species grown in the field abandoned 4 year ago.

Species	Class	Plot A (P-A)		Plot B (P-B)	
		Ind. No.	Sht./Ind.	Ind. No.	Sht./Ind.
<i>A. montana</i>	1	3 (33.3)	1.0	11 (28.9)	1.0
	2	2 (22.2)	1.0	10 (26.9)	1.0
	3	0 (0.0)	—	0 (0.0)	—
	4	4 (44.5)	25.8	17 (44.8)	23.5
	Total	9(100.0)	—	38(100.0)	—
<i>A. rubripes</i>	1	64 (22.2)	1.0	101 (26.7)	1.0
	2	164 (56.9)	1.0	179 (47.4)	1.0
	3	48 (16.7)	2.7	78 (20.6)	3.7
	4	12 (4.3)	8.5	20 (5.3)	14.0
	Total	288(100.0)	—	378(100.0)	—

Ind. No. and Sht./Ind. show number of individuals and mean shoot number per individual, respectively. Figures in parentheses are percentage of individuals number in each size class to total individuals number.

Class 4: individuals with more than two stems and lateral runners.

Figure 3 exhibits the relationships between $\sum_{i=1}^n (Do^2 \times H)$ and individual biomass, both species

showing high correlations. The four different size-classes here discriminated for convenience correspond well to $\sum_{i=1}^n (Do^2 \times H)$ of individual plants, reflecting different growth stages of each

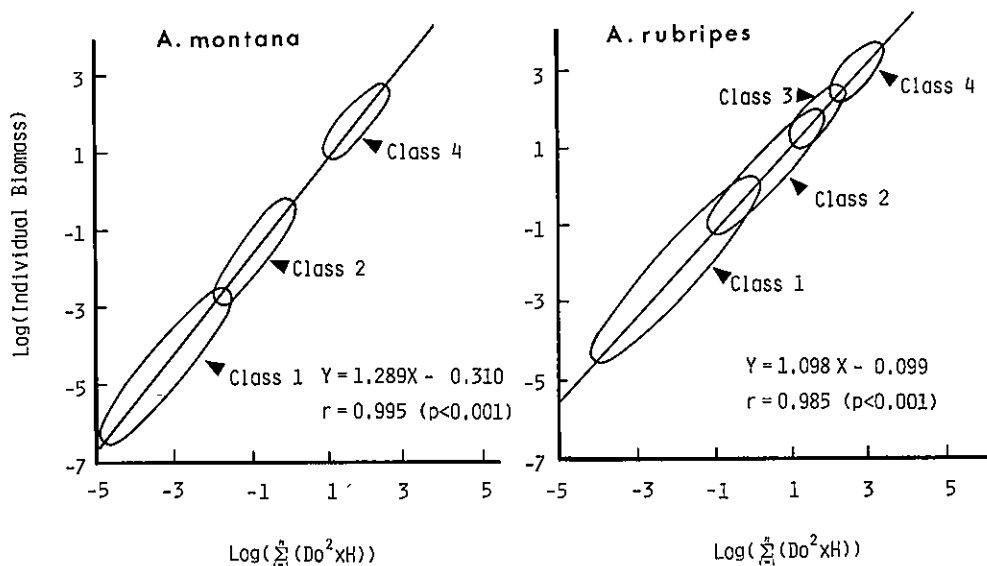


Fig. 3. Relationships between individual biomass and $\sum_{i=1}^n (Do^2 \times H)$ for the two *Artemisia* species. For details of classification of size classes, see text.

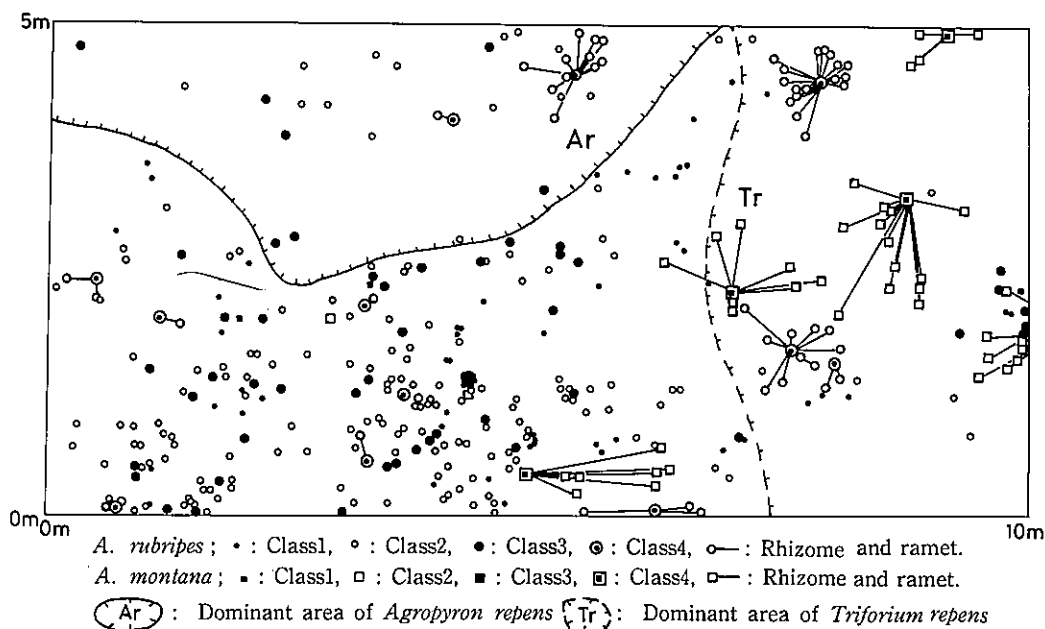


Fig. 4. Spatial distribution patterns of ramets and individuals of two *Artemisia* species in plot A in the old field four years since abandonment.

individual plant.

(2) **Size class structures of populations:** Table 7 shows the size class structures and mean shoot number per individual for each size class sampled from the two plots (Plot A and B), in which small and large patches of *Agropyron repens*, *Trifolium repens*, *Artemisia montana*, etc. were sporadically present. In both plots ($5 \times 10 \text{ m}^2$), *A. montana* showed the highest number of individuals belonging to size class 4, which consisted of exceedingly numerous aerial shoots numbering 24-26 per plant, while fewer plants of smaller size classes were present. On the other hand, *A. rubripes* had a much higher number of individuals belonging to size classes 1 and 2. The individuals of these smaller size classes attained more than 70 % of the total number of individuals; while those of class 4 were the least in number among the all size classes.

There was a marked difference in the mean shoot number per individual of size class 4 between the two *Artemisia* species. *A. montana* produces approximately twice as many shoots per plant as *A. rubripes*. In short, it became evident from these results that *A. rubripes* produces more numerous propagules by sexual reproduction but with less lateral runner growth than *A. montana* in the old field populations.

(3) **Spatial distribution:** Figure 4 shows the spatial distribution of individuals of the two *Artemisia* species in one plot (Plot A). The spatial distribution patterns of the two *Artemisia* species shown in the map may reflect the competitive relationships between the individuals of *A. rubripes* and *A. montana* belonging to four different size classes and clonal expansion of perennial plants such as *Agropyron repens*, *Trifolium repens*, etc. In order to analyze the distribution patterns of *A. rubripes* individuals, IWAO's $m-m^*$ regression analysis (1968) was conducted (Fig. 5). Due to the small number of *A. montana* individuals in Plot A, it was not possible to analyze the distribution pattern for this species.

The larger individuals of *A. rubripes* belonging to size class 4 showed a random or rather uniform distribution. On the other hand, the smaller

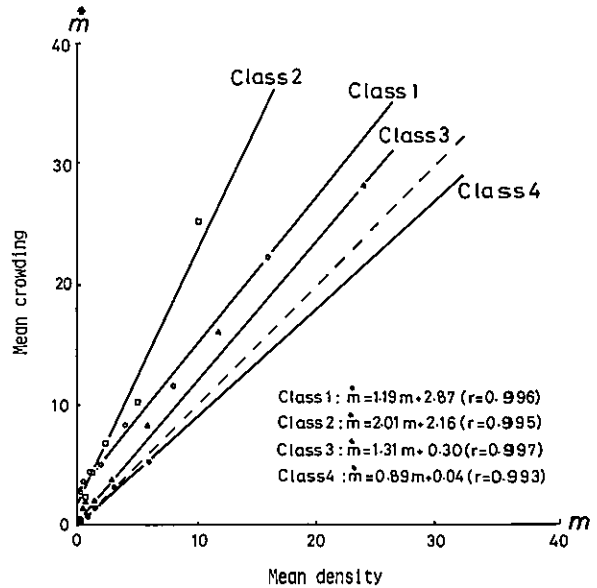


Fig. 5. Distribution patterns of individuals belonging to each size class in *A. rubripes* populations established in plot A. Broken line shows expectation from random (Poisson) distribution.

individuals belonging to size classes 1, 2 and 3 showed an aggregated distribution; those of size classes 1 and 2 especially showed loose clumped structures. The clumps of size classes 1 and 2 also showed a negative association with not only the distributions of *Agropyron repens* and *Trifolium repens*, but also with the individuals of the two *Artemisia* species belonging to size class 4 (Fig. 4). Moreover, those of size class 1 were much less in number and formed smaller clumps than those of size class 2.

It is thus evident from this result that the establishment of seedlings of *Artemisia rubripes* is limited to ecologically vacant places not occupied by any clonally expanding perennial plants. In response to the progress of secondary succession in open habitats of old fields, the vacant patches will diminish gradually and the seedlings of these two *Artemisia* species will also decrease gradually.

Reproductive strategies of the two *Artemisia* species

In *Artemisia rubripes*, the contribution of seed reproduction to the rapid increase of population

size is conspicuously great. On the other hand, in *A. montana* several individuals became very large by clonal expansion but the recruitment from seeds was obviously rare. These differences in the population dynamics of two *Artemisia* species are evident from their population structures in a four year old field (Fig. 4) and also from their reproductive behaviors in experimental populations (NAKAYAMA, submitted). Moreover, judging from the spatial distribution patterns of *A. rubripes*, it is suggested that the recruitment of this species reaches a peak approximately in the third year after a field is abandoned, after which its population size gradually decreases, mainly due to the invasion of other clonal perennial species e. g., *Trifolium repens*, *Agropyron repens*, etc. HARTNETT and BAZZAZ (1985) recently showed that in a typical clonal perennial herb, *Solidago canadensis*, at an old-field in North America, the recruitment also occurs only during the fourth to seventh year after the field is abandoned.

It is now evident that *A. rubripes* occurs more abundantly and dominantly in the old fields (B2 vegetation type) at the late stage of secondary succession than roadsides (B1, B3, and C vegetation types) with moderate human impacts, i. e., trampling (Table 5). In general, crop fields that extend over a wide area in southeastern Hokkaido are plowed at least once a year by agricultural machinery, but once abandoned a secondary succession takes place and it takes usually more than five years until clonal perennial plants invade into and occupy the old fields. During several years in the initial period of secondary succession, populations of *A. rubripes* develop rapidly by means of sexual reproduction. On the other hand, regular artificial disturbances are generally rare on road sides, and thus there is a possibility for some perennial plants to remain as rhizomes or segments of root systems in the soil layer of such habitats. Thus, as compared with old fields, ecologically vacant sites may be occupied much more rapidly by other clonal perennial plants than by sexually reproducing *A. rubripes*.

The individuals of *A. montana* grow gradually and expand their cover by continuously producing new shoots rather than establishing new indi-

viduals by seed progeny in the ruderal habitats, while *A. montana* cannot compete well with plant species which are predominant in open areas such as abandoned fields where intensive competition occurs among the precocious annual, biennial or perennial species typical of the early stage of secondary succession, of which *A. rubripes* is an example. Consequently, *A. montana* shows no differences in relative frequency and coverage value between the old fields at the late stage of succession and the roadsides lacking severe human disturbances (Table 5).

HAYASHI and his collaborators studied the growth, reproductive characteristics, and seedling biology of several representative species found in grassland communities in Japan, in relation to the mechanisms of secondary succession of old fields in central Honshu, although they did not pay attention to population dynamics of these species (HAYASHI 1977, TAKAHASHI and HAYASHI 1978, HAYASHI 1979, HAYASHI et al. 1981, FUKUDA and HAYASHI 1982, HAYASHI 1984). They recognized four different stages in the secondary succession, i. e., pioneer stage, winter annual stage, perennial herb stage, and perennial grass stage. One of the *Artemisia* species, *A. princeps*, occurs as a dominant species at the perennial herb stage in Honshu, and this species possesses the following ecological characteristics: light anemochore seeds without dormancy, shade tolerant seedlings, and a high allocation rate of assimilated matter to belowground parts and leaves (HAYASHI 1984). The two *Artemisia* species examined in this study, however, are characterized by seed dispersal and dormancy strategies, and growth characteristics which are different from those of *A. princeps* (NAKAYAMA 1984; submitted; and unpublished data). Therefore, these three *Artemisia* species may occupy slightly different ecological niches in the ruderal habitats, although they occur dominantly at the very similar stage of secondary succession in the old fields of Japan.

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摘 要

植物の種がその地域個体群を維持するのみならず分布域を拡張するに際して、その種がもつ生活史諸特性が重要な役割を果すことは多くの事例でよく知られている。しかしながら、ほふく性の地下茎により個体生長する雑草性の植物では、未だその生活史諸特性の全貌が明確にされるに至っていない。このような植物の生活史戦略を明らかにすることは、高等植物における栄養繁殖の進化生態学的意義を解明する上においても極めて重要である。この研究で扱った2種のヨモギ属植物は、北海道南東部に共存する雑草性の近縁な種で、エゾヨモギ (*Artemisia montana*) は北海道在来種である一方、ヤブヨモギ (*A. rubripes*) は中国大陸からの帰化種とみなされるものである。この研究では、これら2種のヨモギの生活史戦略を明らかにする一環として、北海道帯広市周辺における両種の生育地と放棄して4年目の畑作跡地における個体群構造の違いを明らかにし、さらにこれらの結果に基づき2種の繁殖戦略について論議した。

調査した58のスタンドは、クラスター分析により類似度32.5のレベル (S ϕ RESEN Inter-stand Coefficient) で6つの植生型に分けることが出来た (Fig. 1)。それらの植生型をそれぞれ、A1, A2, B1, B2, B3およびCと名付け、その植生構造並びに立地環境が記載された (Table 1~4)。

人為的な攪乱 (例えば踏みつけや耕起など) を頻繁に受ける植生型A1とA2のスタンドでは、ヤブヨモギがエゾヨモギより出現頻度・優占度共に高かった。他方、厳しい人為的攪乱を受けることの少ない植生型B1, B2, B3およびCのスタンドでは、エゾヨモギとヤブヨモギの出現頻度・優占度は共に高かった。しかしながら、ヤブヨモギの出現頻度と優占度は路傍 (B1, B2, C) より耕作放棄地 (B2) で顕著に高い傾向が示される一方、エゾヨモギでは2つの生育地の間にはヤブヨモギで見られるような違いはなかった (Table 5)。

2種のヨモギのほふく性の地下茎による平面的な個体生長の指標であるRC ratioは、A1を除くすべての植生型で、エゾヨモギがヤブヨモギより高い傾向を示した (Table 5)。

放棄して4年目の畑作跡地 (Table 6) で両種の個体群のサイズクラス構成を調査するため、各個体を任意の4つのサイズ階級に分けた。これらのサイズ階級はよく個体重を反映していた (Fig. 3)。

この耕作放棄地において、ヤブヨモギはエゾヨモギより極めて大きな個体群を形成していた。ヤブヨモギの個体群ではサイズクラス1および2の小さな個体が全体の70%以上の割合を占める一方、地下茎を持つ大きな個体 (サイズクラス4) が全体の5%以下と極めて低い割合を占めるに過ぎない。これに対し、エゾヨモギでは小さな個体 (サイズクラス1と2) が少なく、地下茎を持つ大きな個体 (サイズクラス4) の割合が全体の40%以上を占めていた (Table 7)。

ヤブヨモギの空間分布を調べると、大きな個体 (サイズクラス4) はほぼランダムに分布しているのに対し、小さな個体 (サイズクラス1と2) は集中して分布していた。またこの小さな個体の集中斑は、主にストロンやほふく性の地下茎により旺盛な個体生長をするシバムギ、シロツメクサあるいはエゾヨモギが存在しない裸地に成立していた (Figs. 4と5)。

これら両種の生育地及び個体群構造の違いがこれらのヨモギの繁殖戦略の違いに起因することは明らかである。すなわち、帰化種であるヤブヨモギは、耕作放棄地の二次遷移初期 (多年生草本が未だ侵入していない期間) に、種子繁殖により大量の個体を補充する。しかし、路傍のような生育地では、種子繁殖のための生態的空白のある空間が欠けるために、耕作放棄地に比べ個体の補充率が低く、個体群も極度に小さくなると考えられる。他方、耕作放棄地におけるエゾヨモギの種子繁殖による個体の補充率はヤブヨモギの補充率に比べ極めて低い反面、地下茎による個体拡大は旺盛である。そのため、この種は路傍・耕作放棄地のどちらの生育地でも大群生しているものと解釈される。

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本書は奄美群島の固有種、北限種などを中心に自筆の図入りで記述している。それらは本土で見られないものであるだけに興味がある。また、奄美各地の方言名の記載は狭い面積の島嶼でも同一の植物に多くの呼称があることを知り、紹介者には面白く思われた。

分布については奄美地方はもちろん、本土および台湾や東南アジアに言及し、全体として平易な記述で煩雑にならず、しかも要領よくまとめられている。

(植之原耕治)