

Population biology of *Habenaria radiata* (Orchidaceae) in Far East Russia and Japan

著者	Tatarenko Irina V., Kondo Katsuhiko
journal or publication title	植物地理・分類研究 = The journal of phytogeography and toxonomy
volume	52
number	1
page range	25-36
year	2004-07-25
URL	http://hdl.handle.net/2297/48643

Irina V. Tatarenko¹ and Katsuhiko Kondo²: Population biology of *Habenaria radiata* (Orchidaceae) in Far East Russia and Japan

¹Research and Education Center of Population Biology, Moscow State Pedagogical University, Moscow 129278, Russia; ²Laboratory of Plant Chromosome and Gene Stock, Graduate School of Science, Hiroshima University, 1-4-3 Kagamiyama, Higashi-Hiroshima 739-8526, Japan

Abstract

Demography of *Habenaria radiata* was studied in the Far East Russia and Japan. The populations of the species studied in Russia were always bigger in size than those studied in Japan. Nearly 40% of the Russian plants studied reached the generative stage forming consequently flowers within two years, another 14% did so within three years. Their seeds formed seed banks maintained in nature for at least 1.5 years. Seeds took 2-6 months to develop protocorms. Spatial structure of the population was characterized by the dense clone formation by intensively vegetative reproduction at rates of 30-80%. Such a population established mainly by ramets in Russia was big and dense, while that in Japan was small and scattered. Vegetatively mature plants dominated in most of the populations studied in Russia and Japan. Externally wounded plants appeared sometimes in Japan after heavy rains.

Key words: dynamics, geographical distribution range, *Habenaria radiata*, population biology, reproductive strategy.

Habenaria radiata (Thunb.) Spreng. is a small terrestrial orchid growing in wetlands and sphagnum bogs in the Far East Russia and Japan (Ohwi 1965; Vyshin 1996).

General information regarding the characteristics of population biology of *H. radiata* includes research work on (1) life history strategy such as ontogenesis, reproduction and mycorrhiza studied in the northernmost distribution in Primorye Territory, Russia (Tatarenko 1991, 1995, 1996), (2) reproductive strategy classified as the G 1-V 3 type (Tatarenko and Vakhrameeva 2001) that was characterized by production of numerous seeds which did not have deep dormant period and by the adult plants regularly sprouted lateral shoots extending to ramets of the same age class as the mother plants, (3) population increase by vegetative reproduction under unexpected conditions for sexual reproduction (Tatarenko 1991), (4) symbiotic culture (Takahashi et al. 2000), (5) reintroduction to certain natural habitats after aseptic seeding, propagation and rescue (Ota 2001; Yamamoto

et al. 2001) and (6) vegetative morphology and reproductive mechanisms in nature and axenic culture (Tatarenko and Kondo 2002).

Demographic studies of some orchid species have been made in populations within certain climatic zone (Willems 1982; Tali 1996), but have been rarely made in populations of certain species in different climatic zones and different types of habitats (Tatarenko 1996; Vakhrameeva et al. 1997; Vakhrameeva 2000). *Habenaria radiata* is such an orchid species, which has populations from the northernmost distribution in colder climate in Russia to the southernmost distribution in warmer climate in Japan. It occurs in different types of habitats. The Russian populations have been studied and characterized in detail, while those in Japan, however, have been poorly studied. A comprehensive analysis of populations of the species in wide ranges of climatic zones is necessary to understand population dynamics and adaptive strategy of the species.

Materials and methods

Frequency of asexual reproduction in *H. radiata* was limited by number of meristems in annual shoots. *Habenaria radiata* had usually three axillary buds subtended by the sheaths at the base of the stem (Tatarenko 1996), and an apical meristem, which sprouts flower stalk in generative plants, however stays as dormant in vegetative plants. Germination of those buds was the only way of vegetative multiplication in this species.

In species of tribe Orchideae the lateral shoot sprouted from the axillary bud extended to form a root-stem tuberoid (the term after Dressler 1981). The root-stem tuberoid of *H. radiata* consisted of stolon 5–10 cm long bearing innovation bud at the tip. Root tuber arose on the second internode of this lateral shoot. A plant appeared from a daughter tuberoid in successive year and fully replaced the mother plant. Vegetative reproduction occurred if 2–3 tuberoids developed at once on a mother plant during a growing season. Daughter plants often belonged to the same age group as their mother plants. Some of them were small in size and would take more time to reach the sexual maturation and those ramets were, thus, called “rejuvenated.”

Two populations of *H. radiata* were chosen in the southern part of Primorye Territory, Russia and five populations of the species were chosen in Hiroshima and Aichi Prefectures, Japan (Table 1). Primorye Territory, Russia is covered with the vegetation of deciduous-coniferous mixed forest in humid region and has an annual mean temperature of 4°C, the mean temperature of the coldest month of -12.4°C, the mean temperature of the hottest month of 22°C, duration of the period in temperature below 0°C for ca 130 days and the annual mean precipitation of 850 (maximum 1,300) mm (Gidrometeocenter 1960). In contrast, Aichi and Hiroshima Prefectures, Japan, are covered with the vegetation of temperate deciduous forest in humid region and have an annual mean temperature of 15°C, the mean temperature of the coldest month of 4°C, the mean temperature of the hottest month of 27°C, almost absent is the period of temperature below 0°C, and the mean annual precipitation of 1,554 mm (National Astronomical Observatory

1996). Vegetation coverages and compositions and soil conditions in the habitats of the populations of *H. radiata* studied were shown in Table 1. The populations of the species studied in the Far East Russia consisted of numerous individual plants and were located in the sphagnum substrata in a large flat, sea-side wetland with slightly salted soil. In contrast, the populations of the species studied in Japan consisted of not so many individual plants and were located in the sandy, clay and humus substrata in small boggy wetlands (Table 1).

Classification of vegetation types in the habitats of the populations of *H. radiata* studied in Japan followed Shimoda and Suzuki (1979).

The populations of the species studied were compared here on the basis of the following ten research items: (1) Fruit set (%) was counted and calculated in the Population Nos. 3, 4 and 6 (see Table 1). (2) Mean number of seeds per capsule was counted and calculated on the basis of ten fruits from the Population Nos. 4 and 6 (see Table 1) and followed by standard statistical treatment ($R=0.95$). Seeds from those ripen fruits were placed on the 1×1 mm² quadrat-scaled filter paper in petri-dish for counting under dissecting microscope. (3) In situ seed germination was measured in Japan following Rasmussen and Whigham (1993). Ten ripened fruits harvested in the Population Nos. 4 and 6 (see Table 1) were used for this experiment. A half amount of their seeds was equally divided and put between cloths of nylon mesh and held up with 60 pieces of 35 mm plastic slide mounts and buried 2 cm deep in the substrate in autumn. The other half amount of the seeds was stored in refrigerator at 4°C for six months after the ripe fruits were harvested, and then, was sown in the same way. Experimental plots were located in two different habitats of *H. radiata*. One more plot was settled for the control in a *Sphagnum* bog, where no *H. radiata* grew in the plant community (Table 3). Seed germination as protocorm development, healthy seeds and aborted seeds were counted in every two slides mounts per study site per every month in summer and every other month in winter. (4) Population structure in *H. radiata* was detected regarding plant size group composition and

Table 1. The populations of *Habenaria radiata* in Primorye Territory, Russia and Hiroshima and Aichi Prefectures, Japan studied

Population No.	Locality	Area (m×m)	Type of vegetation in moor or bog*	Vegetation cover (%)	Type of substrate
1	Russia, Primorye Territory, Khasan District, Station Ryazanovka, wetland on the sea-shore	580×700	<i>Carex limosa</i> — <i>Menyanthes trifoliata</i> association	70	Peat moss
2	Russia, Primorye Territory, Khasan District, Station Ryazanovka, swamp on the sea-shore	250×600	<i>Geranium soboliferum</i> — <i>Menyanthes trifoliata</i> association	80	Peat moss, moor
3	Japan, Hiroshima Prefecture, Higashi-Hiroshima City, Hiroshima University Campus, terrace near the pond	10×15	<i>Rhynchospora chinensis</i> — <i>Eriocaulon sikokianum</i> community, <i>Urticularia bifida</i> group	25	moor, iron-rich
4	Japan, Hiroshima Prefecture, Higashi-Hiroshima City, Saijo-Cho, Gouso, Teraoka-Hachiman Shinto Shrine, swamp along stream	15×30	<i>Arundinaria pygmaea</i> — <i>Lycopodium cernuum</i> community, <i>Juniperus rigida</i> group	35	sand
5	Japan, Hiroshima Prefecture, Kouchi-Cho, Nakakura, swamp along stream	15×25	<i>Rhynchospora faberi</i> community, typical group	75	clay and sand
6	Japan, Hiroshima Prefecture, Higashi-Hiroshima City, Futagami, East slope along Pref. Road 67, bog	25×70	<i>Moliniopsis japonica</i> — <i>Ilex crenata</i> community, typical group	80	humus-rich soil, sand
7	Japan, Aichi Prefecture, Toyota City, Watershed, bog	50×100	<i>Alnus japonica</i> — <i>Moliniopsis japonica</i> community, <i>Isachne globosa</i> group	70	humus-rich soil

*Classification of plant communities in wetland or moor in Japan followed Shimoda and Suzuki (1979).

spread of individual plants within the localities was diagrammatically plotted. Size groups of plants could be generally correlated with their growth stages (Rabotnov 1950; Kawano 1970; Uranov and Serebryakova 1976). Four main growth stages were distinguished in plant life cycle: juvenile (j), immature (im), vegetative mature (vm), and generative or sexual mature (g). (5) Sizes of leaves, roots, tubers and stolons were considered to have significance for the growth stage determination and thus, measured and calculated on the basis of 25 individual plants at each growth stages in each population for quantitative comparisons. Ranges of those quantitative characters of the species in the Japanese populations studied were tabulated as Table 2. (6) Ratio of relative numbers (%) of plants of different growth stages was measured in each population during the flowering period of the species. (7) Spatial structure of the *H. radiata* populations studied was calculated after all individual plants were mapped regarding its growth stages on the linear plots 0.2×10 m. Five linear plots were taken in each locality studied. Statistical analysis of spatial structure was calculated by the following formulae suggested by Grigorieva et al. (1977).

The spatial structure of populations was characterized by size and density of plant dimensions. Population density could vary depending on stolon lengths carrying daughter tubers far from

mother shoots. A dimension of plants in certain area, which may consist of ramets and genets is called "locus." The formula showing the degree of locus separation is:

$$D_M = \frac{M_a - M_i}{M_a}$$

where M_a means the average density of plants within a locus, while M_i means average density of plants in space between the loci.

The formula for the degree of locus disjunction is:

$$D_L = \frac{L_i}{L_i + L_a}$$

where L_i means the distance between the neighbour loci, while L_a means the length of locus itself.

(8) Population dynamics was studied in the permanent plots with marked individuals during two growing seasons in Russian populations in 1989–1990 and three growing seasons in the Japanese population Nos. 3, 5 and 6 (see Table 1) in 2000–2002. Annual shoots in the species were renewed every year as a whole part including tubers and roots. Replaced new tubers bearing the innovation buds were carried by stolons 5–10 cm distance away from the mother shoot (Kumazawa 1956; Tatarenko 1996). Thus, the flag marker indicating the mother shoot on the permanent plot could not indicate the successive daughter shoots. Because of this vegetative behavior, the following methods were applied to in-

Table 2. Quantitative characters of growth stages in *Habenaria radiata* in the populations studied in Japan

Character	Growth stages*			
	j	im	vm	g
Leaf number	2–3	2–3	3–4	3–4 (5)
Leaf length (cm)	1.47–2.51	2.27–4.1	5.8–6.2	6.26–6.7
Leaf width (cm)	0.24–0.31	0.42–0.45	0.51–0.57	0.62–0.66
Root number	1–2	3–4	5–6	5–7
Root length (cm)	1.8–2.7	3.2–4.3	4.5–6.3	5.2–7.4
Stolon number	1	1 (2)	2–3	2–3
Stolon length (cm)	0.8–1.3	2.1–2.96	4.5–8.8	5.2–10.1
Tuber diameter (cm)	0.15–0.23	0.3–0.41	0.52–0.81	0.57–0.86

* "j"=juvenile; "im"=immature; "vm"=vegetatively mature; "g"=generative plants.

investigate population dynamics. All dying mother plants with their new tubers were dug out in the 1 m² quadrat in autumn, and immediately daughter tubers were buried into the substrate in the same depth, and every tuber was marked by flag. Each new tuber was flagged according to the size-group of mother shoot. In the next summer, number and growth stages of shoots produced were recorded for these marked tubers. This experimental procedure of tuber marking was repeated at every autumn during the course of investigation. (9) For the study of seasonal population dynamics in *H. radiata* the growth stage structure of populations were detected twice during one growing season in the permanent plots of the Japanese Population Nos. 3 and 5 (Table 1). Those individuals were flagged in the middle of June, 2000 according to their growth stages. Re-observation was made in the same plots in the middle of September, 2000. (10) Twenty samples of substrates (20×20×10 cm) in each habitat of *H. radiata* were taken to the Laboratories to find out if any protocorms and dormant tubers of the species occurred.

Results

Sexual reproduction

Each adult plant of *H. radiata* usually produced one flower. More vigorous plants, less than 2% of each of the populations studied, had 2–3, rarely 4 flowers. Fruit-sets of individual plants in Japan reached 66.6–88.1%. However, numbers of their final ripe-fruits in some of the

populations decreased dramatically and sometimes fell down to zero since their immature, green fruits were eaten and damaged by insects and slugs. Mean number of seeds per fruit in the species was 1584±83. However, 5.3±2.1% seeds in each capsule had abortive embryos.

The experiment on the in situ seed germination of the species showed the first occurrence of protocorms 1–2 months after seeds were sown in autumn or in the next spring (Table 3). No seed germinated in winter. June and July were the best period of seed germination, since 7–57 protocorms in each sample slide were counted. However, 4.5 to 28% of the seeds used died. Approximately 30% of another sown seeds withheld any visible growth for more than 1.5 years but finally, they indicated no new protocorms development. Such a prolonged latent period was observed in spite of the swelling embryos that began to split the testas of seeds 1–2 months after sowing. There was no significant difference in seed germination between the bog where *H. radiata* grew as a member of the plant community and the other bog where the species did not grow (Table 3).

In all populations studied, neither underground protocorms nor dormant tubers of *H. radiata* were observed naturally in the substrate samples collected in early July. Seventeen protocorms were, then, visible in population No. 5, and 59 protocorms in the population No. 3 in Hiroshima Prefecture in late July to middle August when they produced above ground leaves to be

Table 3. Seed development of *Habenaria radiata* in in situ experiments in natural habitats in Higashi-Hiroshima

Popula- tion No.*	No. of seeds per mount	Protocorm no. one month after sown	Protocorm no. two months after sown	Protocorm no. in June–July	No. of dead seeds in June–July (%)	No. of alive seeds 1.5 years after sown (%)
3	212+38	3**/ 17***	5/9	23/19	4.5	32
6	153+21	0/5	7/7	47/32	28	27
Control	167+11	1/3	9/12	12/25	19	5

The methodology of study followed Rasmussen and Whigham (1993). *See Table 1 for locality descriptions of Population Numbers. Control=ex situ experiment in a sphagnum bog with no plant of *Habenaria radiata* in plant community in Higashi-Hiroshima, Japan. ** / *** =**sown in autumn/**sown in spring.

come juvenile plants. Each protocorm produced two green leaves, the first juvenile tuberoid, and sometimes, adventitious roots.

Asexual reproduction

Eighty to 90% of the mature and healthy plants growing in the Populations Nos. 3, 6 and 7 (Table 1) produced ramets. However less than 4% of the juvenile plants formed more than one daughter tuberoids.

Habenaria radiata produced tuberoids. However, if plants of the species grew in unfavorable habitats such as those in the Population Nos. 4 and 5 (Table 1), they decreased significantly their stolons in length. Their root tubers seemed to be seated on the stems of mother plants although they did not change the other morphological characteristics of their tuberoids. Sometimes, *H. radiata* also form root-stem tuberoids from apical meristems of the vegetative plants.

Since plants of *H. radiata* in Japan often grows along small streams in wetlands, they could be easily damaged by strong water flood after heavy rain. During the course of investigation, 232 externally wounded plants in which old tubers or roots or leaves were broken were observed in the Population Nos. 3 and 5 (Table 4). Thus, 32% of the externally wounded plants survived and formed very small, young tuberoids by autumn. Five externally wounded plants formed

tuberoid with no stolon from apical buds, and two others showed clusters of tuberoids appearing from one axillary bud. Stressful conditions would stimulate the development of axillary buds into the lateral branches with green leaves, which later produce young tuberoids with no stolon.

Growth stage structure of populations

Growth stage structure in populations of *H. radiata* were determined by using the approach of biological age stages (Table 2). Ratio of relative number of plants among the growth stages was considered as an age-state composition of certain population (Table 4). Externally wounded plants found in two populations were counted and calculated as a distinct group which was not due to those plant ages but due to external wound of plant bodies damaged by strong water flood. Especially large number of those externally wounded plants in the Population No. 3 exhibited its unusual composition for this species. Number of generative plants in the Population No. 7 (Table 4) exceeded other growth stages. Total number of plants in the population was rather low, that would be caused by extensive growth of shrubs and grasses under a succession.

The plants of vegetatively mature growth stage predominated in most of the populations studied in Russia as well as in Japan (Table 4).

Table 4. Relative appearance numbers (%) of plants of different growth stages in the populations of *Habenaria radiata* studied in Russia (1 and 2) and Japan (3-7)

Population No.*	Growth stage				Externally wounded plants	Total no. of plants	Density	Relative no. of plants in locus (%)	D _M	D _L
	j	im	vm	g						
1	10	21	51	18	—	2217	255	89.6	0.97	0.50
2	10	31	49	10	—	1990	185	89.2	0.95	0.50
3	13.5	16.5	23	23	24	593	167	17.8	0.89	0.79
4	5	9	75	11	—	139	6.6	12.3	0.9	0.86
5	8	19	52	14	7	377	387	76.25	0.93	0.95
6	9	29	47	15	—	143	301	42.8	0.97	0.94
7	0	8	36	56	—	46	15	43.6	0.999	0.83

*See Table 1 for explanations of Population Numbers. See Table 2 for explanations of growth stages of j, im, vm and g. Externally wounded plants mean plants damaged by water flood. Density means plant number per 1 m². Relative number of plants in locus (%) was calculated by number of plants in locus/total number of plants in population. "D_M" means degree of locus separation. "D_L" means degree of locus disjunction.

Annual dynamics of growth stage structure in populations

Maximum number of plants died at the juvenile age-class during the winter period, while all the plants in the vegetative mature group survived (Table 5). Nearly half of the immature and vegetative mature plants stayed at the same growth stage until next growing season. Fifty-eight to 68% of juvenile plants grew up to the immature age state, and furthermore 8–10% grew up even to the state of vegetative mature state. This observation indicated that they had high speed of ontogenesis in their young plants. Thirty-three to 45% of the immature plants increased their sizes and became vegetatively mature plants. Twenty-five to 30% of vegetatively mature plants produced inflorescence and grew up to generative state, while nearly the same number of plants decreased a little bit their sizes to become immature-like “rejuvenated.” 42.8% of generative plants which flowered in 2000 continued to flower in following year. The

other generative plants had a period of rest, they did not produce any inflorescence and thus, increased the vegetative part of the population (Table 5). In 2002, however, only 13.8% of those generative plants continued to set flower, 5.4% died, and nearly 66% held the vegetatively mature state.

Although plants of the species changed annually from one growth stage to another growth stage (Table 5), general ratio of the growth stages in the whole populations was not altered much during the course of investigation. Thus, the population dynamics of the species in the populations studied in Far East Russia in 1989–1990 were as low as those in the populations studied in Japan in 2000–2002 (Fig. 1).

Seasonal dynamic of the growth stage structure in populations

In the Population No. 3, 22 new juvenile plants appeared from protocorms, three generative and two immature plants died during the

Table 5. Annual dynamics of relative appearance numbers (%) of plants of different growth stages averaged in the Population Nos. 3, 5 and 6 of *Habenaria radiata*. (A) Differentiation from the first year (2000) to the second year (2001). (B) Differentiation from the second year (2001) to the third year (2002)

(A)

Growth stages of plants					
1st year observed (2000)	2nd year observed (2001)				
	dead	j	im	vm	g
j	12	8	58	8	0
im	9	0	48.5	33.3	6
vm	0	0	23.8	52.4	23.8
g	7.2	0	7.2	42.8	42.8

(B)

Growth stages of plants					
2nd year observed (2001)	3rd year observed (2002)				
	dead	j	im	vm	g
j	18.3	2.4	68.3	10	0
im	11.1	0	41.2	45.7	2
vm	0	0	15.1	49.5	35.4
g	5.4	0	14.6	66.2	13.8

See Table 2 for explanations of j, im, vm and g.

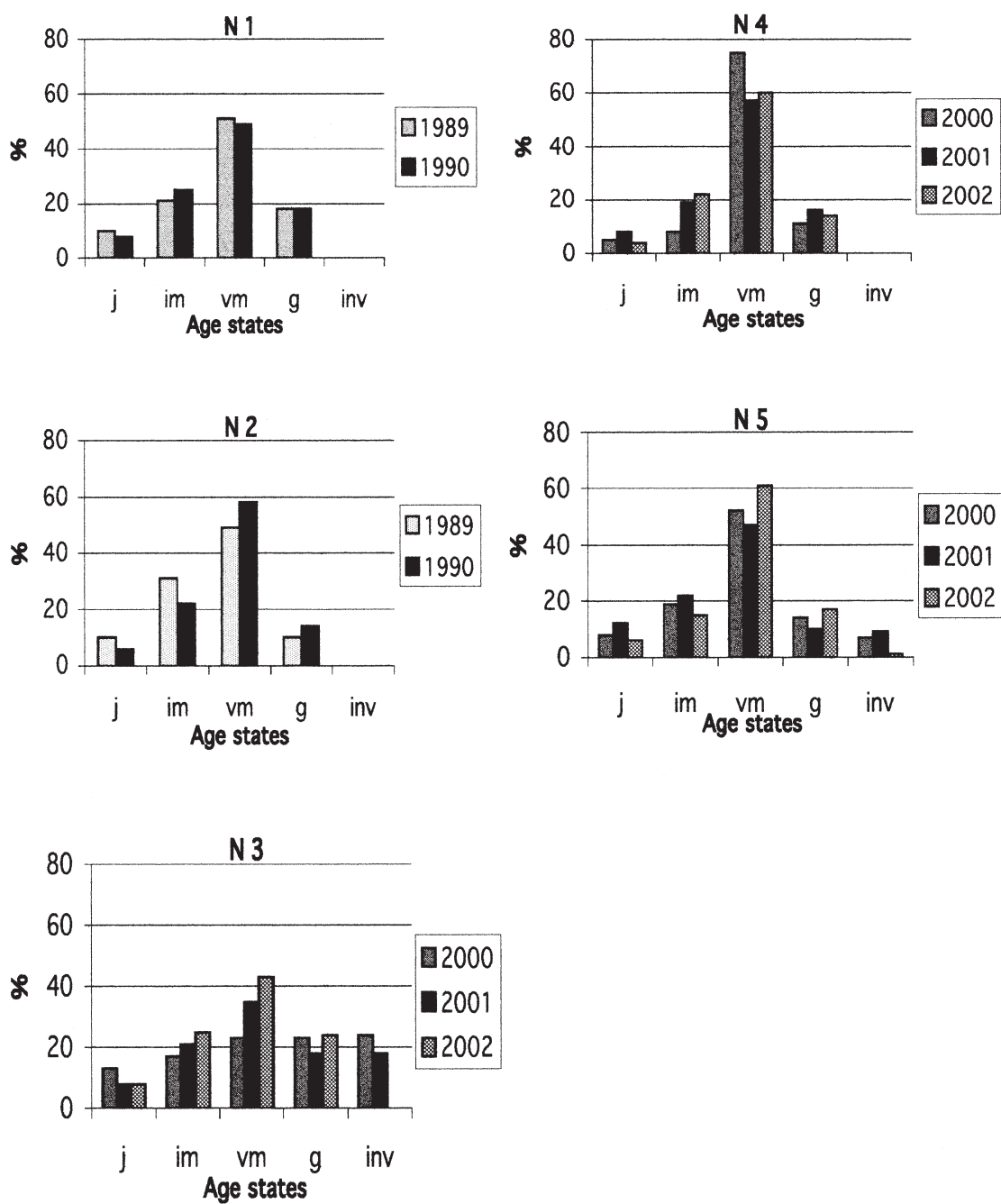


Fig. 1. Annual dynamics of relative frequencies (%) of plants in different age states in populations of *Habenaria radiata* in the Population Nos. 1-5. See Table 2 for explanation of the age states of j, im, vm and g. "inv" means externally wounded plants.

summer period, and did not produce new tubers. Most of the immature and juvenile plants increased leaf numbers and their sizes to grow up to the vegetative mature and immature growth

stages, respectively. However, vegetatively matured and generatively adult plants did not change their sizes and their growth stages during the summer period. In the Population No. 5,

17 new juvenile plants appeared from protocorms, among the juvenile plants that existed in a population from the beginning of summer five plants died, and the others increased their sizes to grow up to the immature growth stage. Thus, most of the plants in the juvenile and immature growth stages changed their leaf numbers and sizes during the summer, and grew up to the next growth stage. Adult plants did not grow up and stayed at the same growth stages or died.

Spatial structure of populations

In habitat of the Population Nos. 4 and 5 (Table 1) where stolon lengths of *H. radiata* plants decreased down to 1.5–2.7 cm, clone density reached 32 plants per 9 cm². In contrast, in more favourable condition where stolon lengths of the species grew up to 7–10 cm, clone density was lower (Table 4). Concentration extent of plants of *H. radiata* in dimensions or population loci in the populations studied in Japan depended on their habitat conditions (Table 4). Degree of locus separation seemed to be less variable among the populations studied (Table 4), and plants within loci in all the study sites were densely concentrated.

Habenaria radiata in the Russian populations studied showed that nearly 90% of the plants were located in dimensions. Each of them was well distinguished from the others and its locus length was equal to the distance between them ($D_L=0.5$). In contrast, in the populations studied in Japan the distance between loci was several times more than locus size. In the Population No. 5, 76% of the plants occurred in dimensions and distance between plants was approximately ten times more than dimension length ($D_L=0.95$). In the Population Nos. 3 and 4, the plants of *H. radiata* were mostly scattered and showed several dense dimensions ($D_M=0.9$) but distantly far location among them ($D_L=0.86$).

Discussion

Sizes of plants at different stages in the populations of *H. radiata* studied in Japan (Table 2) were not much different from those investigated in Far East Russia. Analysis of annual dynamics in growth stage structure of the populations of *H. radiata* studied showed that general ratio of dif-

ferent growth stages fluctuates slightly in successive years (Fig. 1). Vegetatively mature individuals dominated in number in most of the populations of *H. radiata* studied (Table 4). Age structure of the populations changed more during a growing season, especially if some environmental agents disturbed plants. Thus, population structures were changed dramatically after water floods in some habitats in Japan. This occurred during a rainy season in every summer, and caused mass appearance of severely damaged plants in populations located along the streams. This phenomenon has been seen for the first time in the *H. radiata* populations studied in Japan but it has never been seen in any population of the other terrestrial orchids studied up to the present.

Life cycle in *H. radiata* studied in both Japan and Russia, especially that in the young growth stages such as the juvenile and immature stages progressed commonly fast. Seed dormancy did not last more than 1.5 year (Table 3). The most extent of seed germination occurred next summer after seed dispersal from the fruit. Protocorms produced foliage leaves in the same growing season, and became juvenile plants. Some individuals might switch from juvenile to immature and vegetatively mature growth state within next growing season (Table 5).

Wells (1981) stated that plants should reach a critical size to flower. This Wells' statement could be adopted to the orchids which had root tubers to get enough sizes of tubers for flowering. *Habenaria radiata* observed started to set flowers if tubers reached 0.45–0.92 cm diameter. Our observations on plants of different growth stages in the species forced us to speculate that the genet plant could start to set flowers at the 4–5 years stage after seed germination in nature. This reproductive strategy of the species was changed under cultivation where plants started flowering within ten months after seeds were sown (Nagayoshi 1996). The life cycle in the individual plant of the species might take 5–10 years to bring to completion.

Sexual and asexual reproductions were not in contradiction, but rather constituted an essentially inseparable system in the life history of plants (Kawano 1975). Vegetative propagation

was dominated often in place of seed propagation as an insurance mechanism, when the latter was not effective, and plant input saved nutrients for the former one (Serebryakov 1952; Kawano 1970). Both sexual and asexual reproductions were very effective in *H. radiata*. For instance, one of the most vigorous plants had four fruits and three young daughter tuberoids. More than 85% of the plants studied formed fruits and developed 2–3 daughter tuberoids in the Population Nos. 3, 6 and 7. Thus, the energetic resources in the mature plant of the species seemed to be sufficient to hold both sexual and asexual reproductions. However, their juvenile plants were too weak and small to hold vegetative reproduction.

Differences between efficiencies of sexual and asexual reproductions in mature plants of the species were observed among the populations studied. High frequencies of fruit sets were seen everywhere in the populations studied in Japan. Artificial pollination in the species made successfully 100% fruit sets (Nagayoshi 1996). The plants of the species in the populations studied in Russia showed frequency of 60% in natural fruit set and 1814 ± 54 seeds per capsule (Tatarenko 1996).

The intensity of vegetative propagation was changed depending on types of soil substrates in the populations of the species studied. It was less than 17% in poor sandy soil in the Population No. 4 in Japan, less than 20% in muddy, clay substrate in the Population No. 5 in Japan and about 30% in sphagnum substrate in the Population Nos. 1 and 2 in Russia. Oligotrophic substrates seemed to perform decrease of vegetative propagation of the species perhaps due to utilization of limited nutrient resources to sexual reproduction.

The vegetative growth of *H. radiata* promoted not only vegetative reproduction to increase numbers of plants in populations but also spread of daughter plants to new areas by long stolons carrying daughter tubers. For instance, stolon lengths in the species in favourable habitat condition extended to 10–15 cm long, however, those in unfavourable habitat conditions or in physical damage got shortened. Some axillary buds might develop lateral shoots bearing foliage leaves in-

stead of stolons, and apical buds might form tuberoids. Some plants of *H. radiata* formed clusters of new tubers on their apical or lateral buds. These phenomena might be morphogenetic response of plants against the stresses. Stolon lengths in *H. radiata* would be an indicator of plant vigorousness in favourable habitat condition. Thus, all of the plants in the Population No. 7 had stolons more than 10 cm long, while plants in the Population No. 5 had short stolons 2.7 cm long in average and 5 cm long in longest extreme.

Spatial structures of *H. radiata* populations changed every year after the daughter shoots appeared on a new place, more or less far from the mother shoots localization depending on the length of stolons. This phenomenon was named “vegetative mobility” in the most standard Russian references. Lengths of stolons finally determined the density of population loci (Table 4). Relative number of plants concentrated within a locus was considered to depend on both micro relief in a site and period of population growth in the habitat (Tatarenko 1997). The Russian populations of the species studied were bigger in total number of plants, most of individuals were concentrated into loci, and loci were well separated from each other (Table 4). This indicates the long-term existence of *H. radiata* populations in their localities, as well as well-separated elements of micro relief. In Japanese populations of the species loci were less disjuncted, because the micro reliefs of habitats were more flat and smooth. In Population No 5 only the percentage of plants concentrated into loci was more than 70%, whereas in other Japanese populations studied individuals were spread more evenly in the areas of habitats (Table 4). This might be explained by rather young age of populations, in which the dense clones have not appeared yet.

Growth stage composition and spatial structure in *H. radiata* populations growing on the slope on sandy soil along the stream were unusual after some plants were hit and relocated and shifted to surroundings in different places and damaged by water flood. For instance, localization of plants in the Population No. 3 was oriented along the stream and small loci occurred in the spots where invalid plants carried by

water were caught and fixed among grass roots or stems, and regrew there. Thus, the factor of water flood could influence some *H. radiata* populations in Japan. Such externally wounded plants were not found in the populations of the species studied in Russia.

Habenaria radiata and some European orchids with spherical tuberoids had similar growth habits to each other (Tatarenko 1996) but were different in dormancy of tuber from each other. *Habenaria radiata* did not have dormant tubers: Neither tubers flagged on the permanent plots stayed dormant for next growing season, nor such tubers were found in the substrate samples purposely studied during the course of investigation. European *Orchis simia* Lam. had tubers dormant for two years (Willems 1982) and another European *O. militaris* L. had dormant tuber for 3–8 years (Hutchings et al. 1998; Waite and Farrel 1998).

The populations of *H. radiata* studied were quite stable in the range of habitats observed both in Russia and Japan.

Acknowledgements

We would like to thank gratefully the Japan Society for Promotion of Science (JSPS) for supporting Tatarenko by the JSPS Invitation Fellowship (L 00565) for research in Japan during the fiscal year of 2000. The research was also partly supported by Grant-in-Aid for Scientific Research Program (A) (1) 14255014 (Representative Katsuhiko Kondo) from JSPS during the fiscal year of 2002. Special thanks are due to Ms. Suzue Kondo, Nagoya for her kind permission for studying *Habenaria radiata* in Kondo's private property in Toyota City.

References

- Dressler, R. L. 1981. The orchids: Natural history and classification. 332 pp. Harvard Univ. Press, Cambridge.
- Gidrometeocenter (ed). 1960. Agroclimaticeskij spravochnik po Primorskemu krayu. 130 pp. Gidrometeocenter, Leningrad. (in Russian)
- Grigorieva, N. M., Zaugolnova, L. B. and Smirnova, O. V. 1977. Peculiarities of spatial structure of cenopopulations in some plant species. Uranov, A. A. and Serebryakova, T. I. (eds.). Coenopopulyacii rasteniy, pp. 20–36. Nauka, Moscow. (in Russian)
- Hutchings, M. J., Mendosa, A. and Havers, W. 1998. Demographic properties of an outlier population of *Orchis militaris* L. (Orchidaceae) in England. Bot. J. Linn. Soc. London **126**: 95–107.
- Kawano, S. 1970. Species problems viewed from productive and reproductive Biology I. Ecological life histories of some representative members associated with temperate deciduous forests in Japan – A preliminary discussion. J. Coll. Lib. Arts, Toyama Univ. **3**: 181–213.
- Kawano, S. 1975. The productive and reproductive biology of flowering plants. II. The concept of life history strategy in plants. J. Coll. Lib. Arts, Toyama Univ. Nat. Sci. **8**: 51–86.
- Kumazawa, M. 1956. Morphology and development of the sinker in *Pecteilis radiata* (Orchidaceae). Bot. Mag. Tokyo **69**: 455–461.
- Nagayoshi, T. 1996. Multiplication and breeding of Japanese wild orchid *Habenaria radiata* (Thunb.) Spreng. Proceedings of 5 th Asia Pacific Orchid Conference, pp. 225–227. Organizing Committee for APOC 5, Fukuoka. National Astronomical Observatory (ed.). 1996. Chronological scientific tables 1996. 1043 pp. Maruzen, Tokyo.
- Ohwi, J. 1965. Flora of Japan. 1067 pp. Smithsonian, Washington, D.C.
- Ota, K. 2001. Re-introduction of *Habenaria radiata* to the marshy area in Gifu Women's University. Proceedings of the 7 th Asia Pacific Orchid Conference, pp. 196–197. Secretariat of APOC 7, Nagoya.
- Rabotnov, T. A. 1950. Life cycle of perennial herbaceous plants in meadow ceonosis. Trudi Bot. Inst. Acad. Nauk USSR, Ser. 3, Geobot. **6**: 7–204. (in Russian)
- Rasmussen, H. N. and Whigham, D. 1993. Seed ecology of dust seeds in situ: a new study technique and its application in terrestrial orchids. Am. J. Bot. **80**: 1374–1378.
- Serebryakov, I. G. 1952. Morphology of vegetative organs of higher plants. 391 pp. Sovetskaya Nauka, Moscow. (in Russian)
- Shimoda, M. and Suzuki, H. 1979. Wetland vegetation of the Saijo Basin Hiroshima Prefecture. Phytosoc. Soc. Japan **16**: 315–323.

- Takahashi, K. I., Ogiwara, N. and Hakoda, N. 2000. Seed germination of *Habenaria (Pecteilis) radiata* (Orchidaceae: Orchideae) in vitro. *Lindleyana* **15**: 59–63.
- Tali, K. 1996. Spring-flowering and summer-flowering populations of *Orchis ustulata* L. (Orchidaceae) in Estonia: Their comparison and distribution. *J. Eur. Orchideen* **28**: 573–582.
- Tatarenko, I. V. 1991. Orchids of Primorye Territory, Russia: Biology, ecology, protection. PhD Dissert., Moscow State Univ., 24 pp. (in Russian)
- Tatarenko, I. V. 1995. Mycorrhiza of orchids (Orchidaceae) in Primorye Territory, Russia. *Bot. Zhurn.* **80**: 64–72. (in Russian)
- Tatarenko, I. V. 1996. Orchids of Russia: Life forms, biology and strategy of preservation. 207 pp. Argus Publ., Moscow. (in Russian)
- Tatarenko, I. V. 1997. Spatial structure of orchids with root-stem tuberoids. *Bull. Moscow Soc. Nature Explorers, Div. Biol.* **93**: 54–57. (in Russian)
- Tatarenko, I. V. and Kondo, K. 2002. Vegetative morphology of *Habenaria radiata* (Orchidaceae) in nature and axenic culture. Proceedings of the 2nd International Conference on Plant Anatomy and Morphology, pp. 326–327. *Bot. Inst. RAN, St. Petersburg.*
- Tatarenko, I. V. and Vakhrameeva, M. G. 2001. Demography and reproduction strategy of some terrestrial orchids of Russia. Proceedings of the 7th Asia Pacific Orchid Conference, pp. 42–44. Secretariat of APOC 7, Nagoya.
- Uranov, A. A. and Serebryakova, T. I. (eds.). 1976. *Coenopopulacii rasteniy.* 216 pp., Nauka, Moscow. (in Russian)
- Vakhrameeva, M.G. 2000. Genus *Dactylorhiza*. Pavlov, V. N. (ed.). *Biological flora of Moscow Province* Vol. 14. pp. 55–86. Gifi Ko, Moscow. (in Russian)
- Vakhrameeva, M.G., Varlygina, T. I., Batalov, A. E., Timchenko, I. A. and Bogomolova, T. I. 1997. Genus *Epipactis*. Pavlov, V. N. and Tikhomirov, V. N. (eds.). *Biological flora of Moscow Province.* Vol. 13, pp. 50–87. Polieks, Moscow. (in Russian)
- Vyshin, I. B. 1996. *Orchidaceae* Juss. Khark-
evich, S. S. (ed.). *Vascular plants of Soviet Far East* Vol. 8, pp. 301–339. Nauka, St. Petersburg. (in Russian)
- Waite, S. and Farrel, L. 1998. Population biology of the rare military orchid (*Orchis militaris* L.) at an established site in Suffolk, England. *Bot. J. Linn. Soc. London* **126**: 109–121.
- Wells, T. C. E. 1981. Population ecology of terrestrial orchids. Synge, H. (ed.). *Biological aspects of rare plant conservation*, pp. 281–295. John Wiley and Sons, Chichester.
- Willems, J. H. 1982. Establishment and development of a population of *Orchis simia* Lamk. in the Netherlands, 1972–1981. *New Phytol.* **91**: 757–765.
- Yamamoto, T., Saito, Y., Yamamoto, C. and Kinjo, N. 2001. Reintroduction and restoration of population of *Habenaria radiata* in natural habitat by plants propagated by aseptic seeding. Proceedings of the 7th Asia Pacific Orchid Conference, pp. 48–50. Secretariat of APOC 7, Nagoya.

(Received September 12, 2003; accepted January 19, 2004)

イリナ V. タタレンコ¹・近藤勝彦²: 極東ロシアと日本におけるラン科サギソウの個体群生物学

極東ロシアと日本の異なった生育環境でのサギソウの個体群動態を観察、比較した。極東ロシアの個体群サイズは日本のものより常に大きかった。極東ロシアの個体のうち、生殖期に達した約 40% は 2 年で花をつけ、14% は 3 年で花をつけた。それらが生産した種子は少なくとも 1.5 年間地面で休眠した後、2–6 ヶ月かかってプロトコームとなった。個体群の空間的拡がりには、主にクローン繁殖のための地下茎の長短によりできる娘塊茎の位置の違いに依り、30–80% の集中的クローン繁殖力によりできる高い密度により特徴づけられた。極東ロシアで観察したそのようなクローン中心の個体群は大きく、そして密集していたが、日本で観察した個体群は小さく、疎であった。十分に栄養成長した植物個体は、極東ロシアと日本の調査個体群の殆どで優占していた。日本での観察個体群の一部で、大雨の後に外傷個体を多数観察した。

¹ロシア連邦モスクワ市 モスクワ国立教育大学個体群生物学研究教育センター; ²〒739-8526 東広島市鏡山 1-4-3 広島大学大学院理学研究科附属植物遺伝子保管実験施設)