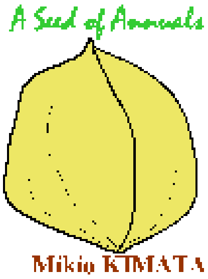
Chapter 2: Plants and people in the Quaternary



Most people are very interested in the ancestral species of domesticated plant, but they never know the domestication process among plant and human being. They are not curious about our coevolution between plants and human being. Then I have conducted botanical experiment and field research on growth habit, reproductive system such as very important characteristics on the domestication process. I did not apply only to Poaceae, also I used some genera for comparative studies on growth habit and reproductive system. Moreover, I had done form ecogenetical study to molecular analysis of biological component.

Comparative ecological genetics on annuals and perennials

Nakao (1967) and de Candolle (1883) had suggested that the research on the evolution of annual was very important for explaining the origin of domesticated plant. I had known now that their excellent idea had been connected with my issue of doctoral thesis (Kimata 1980) ‘Studies on the Comparative ecogenetics of annual and perennial plants.’ Sakamoto had given me the ecogenetical study on the aspect which annual had evolved from perennial.

As shown the evolution of plant in Figure 2, the C_4 plants had emerged in tertiary era, about 7 million BP, and then the perennial herb had appeared in Neogene. Subsequently the annual herb had appeared in Quaternary, 2.58 million BP. The annuals had survived by seed dormancy under the severe conditions which were cold, hot and drought. The reproductive systems of plants had become remarkably diversified for responding the environmental change. Synchronically, the ancestral genus *Homo* had appeared around Quaternary. Also, the gregarious animals had adapted and settled in grassland.

The most of Perennials I are cross-fertilized and self-incompatible species. Perennials II are cross-fertilized species, or sometimes are able to parthenogenesis. Perennials III are only parthenogenesis. Perennials IV are cross-/self-fertilized and self-compatible. Annuals had evolved from Perennials IV. Annuals are self-fertilized and sometimes cross-fertilized. Annuals can produce numerous seeds. The general characteristics of annuals and perennials are compared in Table 3. However, it is very difficult to say simply, as each plant species have diverse habits.

Evolution from annual to perennial plants

The evolution process of plant growth habit from perennial to annual have been very important, because the grains are mostly annual or annual-like under cultivating condition.

The reproductive systems of annual and perennial species are usually quite different (Baker 1955, 1959, 1974; Stebbins 1957, 1958, 1974; Ehrendorfer 1965; Harper 1967; Antonovics 1968;

Harper and Ogden 1970; Kawano 1974; Jain 1976). The reproductive strategy of annuals is only that of sexual reproduction by seed, while that of perennials is composed of the sexual and/or vegetative modes. Annuals are often self-pollinated, while perennials often cross-pollinated. Moreover, self-pollinating taxa usually appear to have been derived from outcrossing relatives, and annuals from perennials. Generally, it is thought that the homozygous genotypes by inbreeding sacrifice the evolutionary capacity for a change. However, there is another explanation that the evolution of inbreeding is not purely accidental, but is actually favored by natural selection because selfers possess some advantages over crossers under certain conditions.

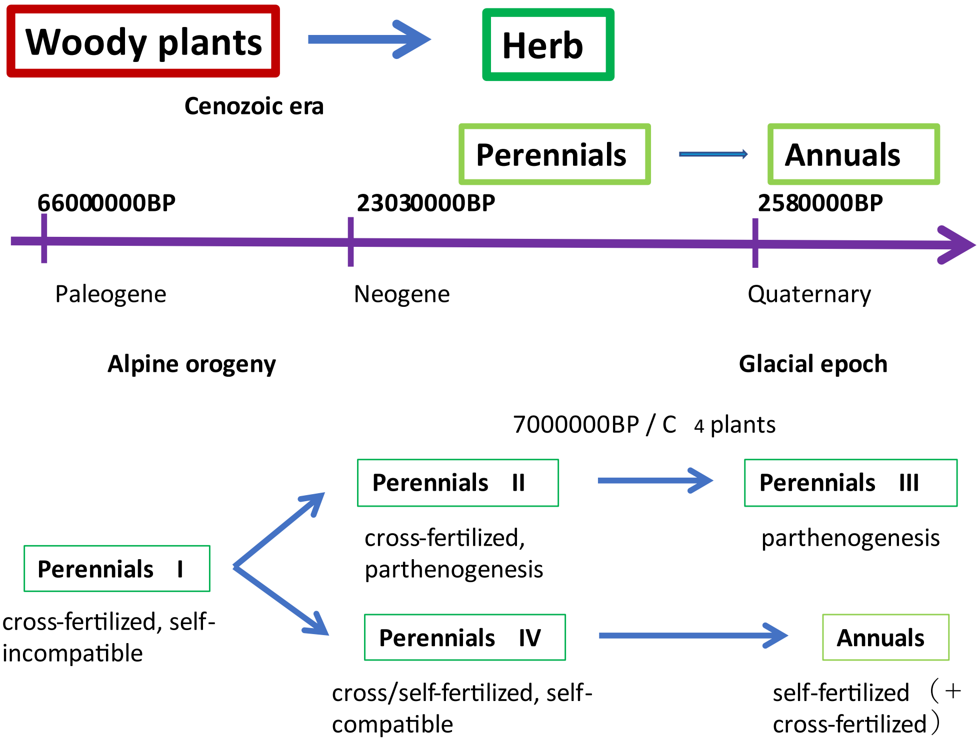


Figure 2. Phylogenetic evolution of herbaceous plants

Roughly speaking, annual plants are self-fertilizers, the flowers are small, whitish, so many, and these produce numerous small seeds as shown in Table 3. The self-fertilization reduces genetical variability, but the polyploidy preserves biodiversity. Annuals colonize into habitats disturbed by nature or human being. The self-fertilization guarantees for becoming a colonizer and pioneer. Most annuals have C_4 pathway and the energy product allocates much to seeds. The phenotype indicates wide range of degrees by the environment. Those characteristics had effectively worked for domestication process.

On the other hand, perennials indicate contrasting characteristics. Perennials are mostly cross-fertilizer, and at the same time they carry out both seed and vegetative reproduction. Those spices are diploid and C_3 pathway in general. In rare cases, the interspecific hybrids between annual and perennial species in same genus are rarely occurred. As some results in the following experiments, perennial was genetically dominant, while annual was recessive. Moreover, *Oryza sativa*, *Coix lacryma-jobi* subsp. *ma-yuen* and *Paspalum scrobiculatum* were botanically perennial, but became ecologically annual and non-shattering through artificial selection.

Table 3. Comparison between annual and perennial reproductive systems

Character	Annual	Perennial
Pollination system	self-pollinated	cross-pollinated (self-incompatible)
Flowers	smaller, monocolored (whitish)	large, polycolored
Pollen grains	fewer	many
Anthers	adjacent to stigma	distant from stigma
Asexual reproduction	absent	present
Flowering	quick	slow
Germination	quick	slow
Sexual reproduction by seed	many	fewer
Seed weight	light	heavier
Polyploidy	high	mostly diploid
Plasticity in phenotype	high	low
Photosynthesis	many C4 pathway	C3 pathway
Habitat	disturbed	stable
Energy allocation	much seeds	vegetative organ,
growth habit	dominant	recessive

In the domestication process as evolution involved artificial and natural selections, the important characters of annual were reproductive systems (self-/cross-fertilized, vegetative), size and number of seeds, photosynthesis circuit (C_4 or C_3), energy allocation, and so on. The annual life cycle of grain crops had been closely related to seed production (Table 4).

Compared with perennials, annuals do not vegetative propagation (few exceptional cleistgamy), have a lot of small whitish flowers by sexual reproduction, and a few pollens for self-fertilizer. Annuals are mostly self-fertilizers (sometimes cross-fertilize), produce numerous seeds, and can make big population through only a seed. The self-fertilization decreases genetic variability, but polyploidy increases and accumulates genetic variability. For example, the self-pollination rate of *Zea mays* is very low, about 5% because of anemophilous flowers and hermaphrodite. *Coix lacryma-jbi* and *Pennisetum americanum* are cross-fertilizers with protogyny. *Sorghum bicolor* is self-fertilizer. Generally speaking, fruits Brassicaceae plants are self-incompatible, they cannot pollinate by own pollens. However, surprisingly the self-pollination rate of *Oryza sativa* is almost 100% in spite of perennial.

Table 4. Comparison between cross-fertilizer and self-fertilizer

	Cross-fertilizer	**Self-fertilizer**
Pollination system	cross-pollination, self-incompatible	self-pollination, self-compatible
Recombination	low	high
Polyploidy	diploid	polyploid
Flower	colorful, aroma, nectar gland, honey beacon	monochromatic, white, degeneration
Pollen	many	few
Fruit	partially fruited	plentiful fruited
Distribution	narrow	wide

Annuals grow in seasonal semi-arid regions for example the savannah or Mediterranean area, and human living area i.e. habitats disturbed frequently in growing environment. Summer annuals are dominant under the savannah climate, local people had domesticated many kinds of millet and then constructed Savannah Agricultural Complex. On the other hand, Winter annuals are dominant under Mediterranean climate, local people had domesticated many kinds of wheat, Triticeae and then constructed Mediterranean Agricultural Complex. Moreover recently, yearlong annuals have adapted to artificial environment under the urban area. Each plant dies after flowering and fruiting within a year, but the population inhabits through all seasons, i.e. yearlong annual, *Mazus japonicus*,

Perennials grow at non-disturbed and stable habitats, in forest, mire, wetland. These reproductive systems are both vegetative and sexual reproduction. They produce a lot of pollens but a few flowers which are bigger and colorful. Perennials sometimes include self-incompatible species, many diploid plants, and a few big seeds.

C_3 plants carry out photosynthesis only by carboxylic acid cycle. Their photosynthetic product is trimonosaccharid (3-sulfoglyceric acid) in the first step. There are so many plants, *Oryza sativa*, *Triticum aestivum*, *Glisin max*, *Brassica napus* and so on. C_4 plants carry out photosynthesis initially by C_4 pathway (dicarboxylic acid cycle) and subsequently by carboxylic acid cycle. These are about 20 families and 3000 species including families Poaceae, Cyperaceae, Amaranthaceae, Chenopodiaceae in the tropical and subtropical zones. The photosynthesis rate of C_4 plants is higher than those of C_3 plants. Moreover, the utilization efficiency of C_4 plants is higher than C_3 plants on water and nitrogen. (https://www.jaicaf.or.jp)

The growth habits of weeds growing in Japan are shown in Table 5 (Kasahara 1974). The rate of native annuals is over 40% of weeds in Japan (344 species including prehistoric naturalized plants), and also the rate of native perennials is about 40%. The rate of naturalized annuals is about 15% and the rate of naturalized perennials is about 6%. On the latter naturalized case, the rate of annuals is 2.5 times more than the rate of perennials. Summer annuals have been companion weeds for rice paddy fields, while winter annuals have been companion weeds for wheat fields. When new coming weeds invaded into disturbed habitats, namely the annuals were advantageous for becoming naturalized weeds.

Table 5. Growth habits of weeds in Japan

Growth habit	Native species	Naturalized species	Total
Summer annual	131 (29.8%)	33(7.5%)	164(37.2%)
Winter annual	32(7.3%)	24(5.5%)	56(12.7)
Summer/Winter annual	13(3.0%)	11(2.5%)	24(5.5%)
Perennial	165(37.5%)	27(6.1%)	192(43.6%)
Perennial/Annual	2(0.5%)	1(0.2%)	3(0.7%)
Tree	1(0.2)	0(0%)	1(0.2%)
Total	344(78.2%)	96(21.8%)	440

Kasahara 1974

The ancestral and relative species of domesticated grain crops have grown all around our habitats as indicated in Figure 3. For example, *Setaria viridis* is the ancestor of *S. italica* and both species make hybrids. *Setaria pumila* is the same species as the ancestor of kolati, *S. pumila* in Eastern India. *Coix lacryma-jobi* subsp. *lacryma-jobi* is the ancestor of *Coix lacryma-jobi* subsp. *ma-yuen*. *Echinochloa crus-gali* is the ancestor of *E. utilis*.

Digitaria iliaris

Coix lacrymaobi

Paspalum thunbergii

Setaria viridis

Echinochloa crus-galli

Penisetum alopecuroides

Setaria pumila

Eragrostis ferruginea

Avena ***fatua***

Hordeum murinum

Sorghum halepense

Agropyron tsukushiense

Figure 3. Weeds relating to domesticated plants in nonboring sites.

Ecological genetics on five genera

Most annual plants have the ability to set many seeds by autogamy (Baker 1974). Moreover, with self-fertilizers a single individual can establish a colony even on a temporarily disturbed habitat long-distance dispersal (Baker 1955, 1959; Stebbins 1957, 1958; Antonovics 1968; Lefébre 1970; Jain 1976).

Perennial species are often cross-fertilized and mostly polycarpic plants which have lived over a year. On the contrary, annual species are the monocarpic which complete their life cycle and die within a year (Harper and White 1974; Harper 1977). The reproductive strategy of annuals is only that of sexual reproduction by seed, with few exceptions, while that of perennials is composed of the sexual and vegetative modes (Baker 1959; Harper 1967; Harper and Ogden 1970; Kawano 1974).

The reproductive allocation of dry matter into the seeds is considerably higher in annuals than in perennials. On the contrary, only in perennials the reproductive allocation into the vegetative propagules or storage organs is often very high (Eherendorfer 1965; Harper 1967; Harper and Ogden 1970; Kawano 1974, 1975; Ogden 1974; Kawano and Nagai 1975).

The seasonal variation in the population density of summer annuals has been studied in both cases in which winter annuals existed and did not exist (Raynal and Bazzaz 1975). However, it has hardly been studied in the sympatric habitat, where annual species have grown with the related perennials.

In an attempt to clarify the ecogenetical characteristics of annual species and their perennial relatives, comparative studies in five genera of the following plants, *Mazus*, a genus of the family Scrophulariaceae; *Cardamine* and *Rorippa*, Cruciferae; *Agropyron Coix, Secale* and *Zea*, Gramineae, were conducted. It is emphasized that these comparative ecogenetical studies in these five plant genera provide some critical information concerning the ecogenetical aspects on the origin of weeds as well as domesticated plants.

Comparison of life history strategy and reproductive system between *Mazus japonicus* and *M. miquelii*, Scrophulariaceae

Family Scrophulariaceae have been dispersed 210 genera and 3000 spices in the world. There are 10 spices of genus *Mazus* in the world and 3 species in Japan (Satake 1964). *Mazus japonicus* (Thunb.) O. Kuntze is an annual weed which has distributed over the temperate or tropical zones from Afghanistan to China and Japan, Shino-Japanese floral region. *M. japonicus* had been naturalized to the East Cost a hundred years ago, but *M. miquelii* had been naturalized about 50 years ago. It is unknown where these species distribute in the United States today (Michener personal communication 1977). *M. miquelii* Makino is a perennial weed which has distributed from Central China to the southern Hokkaido in Japan. *M. faurei* Bon. has grown in the south Kyushu, Okinawa and Formosa (Kitamura and Murata 1964). I have not seen this spices in Kagoshima, Miyazaki and Okinawa. *M. pumilus* (Burm. f) Steenis is a synonym of *M. japonicus*. Moreover, *M. goodcnifolium* (Hornrm.) Pennell and *M. quadriprotuberans* N. Yonezawa (1998) grow in Japan

Mazus japonicus (Thunb.) O. Kuntze was collected and observed in Koganei-shi and Kunitachi-shi, Tokyo, and *M. miquelii* Makino in Hino-shi and Kunitachi-shi, Tokyo. Voucher specimens are deposited at the Herbarium of Tokyo Gakugei University (Figure 4). At the same time in Kunitachi-shi *Vandellia crustaceae* Bentham and V*eronica persica* Poir. were also observed for the comparison with *M. japonicus*. *M. japonicus* (annual) and *M. miquelii* (perennial) grow sympatrically in rice paddy fields. There life history strategies were compared on the base of relation between reproductive systems and population dynamics in the sympatric habitat (Kimata 1978; Kimata and Sakamoto 1979; Kimata).

Figure 4. *Mazus japonicus* and *M. miquelii* on the levee of paddy field

A close relation between the number of blooming flowers and the number of visiting pollinators was observed in *M. miquelii.* On a sunny day the mode of blooming flowers was consistent with that of the frequency of visiting pollinators. The reaction time of stigma seismonasty in *M. miquelii* has a tendency to be longer during the day than during the night, but on the contrary, the recovery time had a tendency to be shorter during the day than during the night. Therefore, it is clear that the stigma lobes close more slowly and open more quickly during the day than during the night. Since most pollinators visit flowers during the day and since stigma seismonasty is lost by pollination, it is assumed that the stigma seismonasty observed in *M. miquelii* is an adaptation to cross-pollination by insects.

The growth habit (annual or perennial) of a given plant species is usually determined through field observation. However, the growth habit can be exactly determined only through experimental studies. If it is an annual species, the plants must die without a dormant bud formation after the flowering and fructification in the natural state. *M. japonicus* did not die through low temperatures or frost but died after fructification. This clearly indicates the annual growth habit of *M. japonicus.* According to field observations of natural populations of this species, individuals in different stages of growth were found in the populations almost all the year round. Seed germination occurs from April to October successively and flowering also takes place similarly. On the contrary, *M. miquelii* is a perennial species because this species produces many ramets through stolon formation. Flowering of this species is mainly controlled by the temperature. The time of flowering was observed twice in natural populations. In the spring from April to May, the plants, produced asexually in the autumn of the previous year, bloom abundantly and produce many seeds in this period. From August to October only, a few plants, germinated in May to June, produce flowers on the top of the stolons. Most plants in natural populations in this period produce many ramets asexually.

The difference of pollination systems in *M. japonicus* and *M. miquelii* is also indicated by the pattern of seed production in these species. A capsule of self-pollinated *M. japonicus* produced more seeds but the variation in the number of seeds was smaller than found in *M. miquelii.* Moreover, seeds of *M. japonicus* were smaller and lighter, and this species may be more adapted to an effective seed dispersal. In *M. miquelii,* on the other hand, a small number of seeds per capsule is produced and the number is more variable than in *M. japonicus.*

There were two flowering seasons in *M. japonicus* which was a year-long annual. The seeds were produced mainly twice in spring and autumn by the plants of winter and by those of summer population, respectively. In the winter population there were two grades of plant size. The number of seeds produced by a summer plant (9,105 grains) was about three times as many as by a small plant in winter population (2,929), but was only about a fifth as many as by a large plant (51,241) which was germinated in summer by chance. Namely, if the mean value of seeds was estimated as an individual in winter population, the number of seeds in a summer plant was approximately as many as that in a winter one. Generally, in a summer population *M. japonicus* produced mostly seeds during autumn because of the high population density, and in a winter population it did many seeds during spring, then the seeds of winter plants germinated and became summer plants.

M. miquelii had two flowering seasons, and in spring produced 3,638 seeds, but in autumn only 60. In spite of 94.2% pollen fertility, the latter plant which formed by seed had just 16.7% seed fertility because of low activity of pollinators under the low temperature condition. Therefore, the seed production of *M. miquelii* was only a third as many as that of *M. japonicus* even in spring.

However, at the same time *M. miquelii* propagates asexually by stolon formation which might compensate for the smaller production of seeds and thereby maintain the natural populations in this species. The plant formed by ramet produced ca. 300 new ramets in May-October. On the other hand, the plant formed by seed could hardly contribute to the magnification of a species population in the first year, because few seeds and small number of ramets are produced by it.

Reproductive systems of two *Mazus* species

Mazus japonicus is a self-pollinated species, while the breeding behavior of *M. miquelii* mostly cross-pollinated with a low degree of self-incompatibility (Table 5). The pollination size of the upper anthers and the pollen fertility of the upper and lower anthers were not important factors because such differences were not statistically significant between the two species. However, it was suggested that the pollen fertility of upper anthers was effectively concerned with self-pollination in *M. japonicus,* since the pollen fertility of the upper anthers was significantly higher than that of the lower anthers at 1% level. The quotient of under-lip length of stigma lobes showed a remarkable difference between the two species. This indicates that the under-lip of the stigma lobes of *M. japonicus* develops markedly. The curved tip of the under-lip of the stigma lobes is self-pollinated by the half wrapping of the upper anthers. On the contrary, *M. miquelii* is not self-pollinated, because the under-lip of the stigma lobes of this species does not develop so much, and the stigma shows stigma seismonasty. Stigma seismonasty has been observed in the Scrophulariaceae, Ranunculaceae, Pedaliaceae, Bignoniaceae, Capparidaceae and Maryniaceae. *M. miquelii* is one of the examples found in the Scrophulariaceae. It has been suggested that this phenomenon is closely related to cross-pollination by insects and to promotion of pollen germination on the stigma (Yoshinaga 1890; Miyoshi 1891; Newcombe 1924; Watanabe 1969).

Table 5. Reproductive systems of *Mazus miquelii* and *M. japonicus*

Species	Spring	Flowering season	Summer	Autamun	Winter	Growth habit
Mazus japonicus	rosette, bolting	winter form flowering,	fuluiting, dead	germination	rosette	
		germination, growth in summer, flowering/fruiting.	germination, growth in summer, flowering/fruiting .dead			year long annual
Mazus miquelii	rosette, bolting	flowering and fruiting, seed germinating	elongating stolons, formating many ramets (vegetative reproduction)	flowering, making rosette, seed germination	rosette	perennial

Population dynamics of annual weeds

There are three types of annual species, e.g., summer, winter and "year-long" annuals. *Vandellia crustacea* is a typical summer annual, for the plant of this species lives from June to November. *Veronica persica* is a typical winter annual, for the plant lives from September to the following June. On the contrary, *M. japonicus* was a summer and winter annual, i.e., a year-long annual because the population has been maintained all year-round, notwithstanding that each individual of the population germinated and died within a year. These three species were all annual species even physiologically.

Veronica persica and *M. japonicus* showed a bimodal pattern of seed germination with two peaks of plant density in November-December and March-April, and in November and June-July, respectively. This phenomenon was observed in *Setaria faberii* Herm. which seemed to have two seed populations differentiated on the basis of time of germination (Raynal and Bazzaz 1975). There is no evidence for yet whether the mortality of *Veronica persica* and *M. japonicus* is dependent upon population density or not. However, their mortality was apparently affected by drought and frost condition.

The population of *M. japonicus* had a long flowering period, nearly all year-round, in spite of being an annual species under the artificial and natural conditions. There were more inflorescences in summer plants than in winter ones. Therefore, most seeds were produced during summer.

As mentioned in the previous section, it is apparent that *M. japonicus* is a self-pollinated species, while *M. miquelii* is a mostly cross-pollinated one with asexual reproduction by stolon. It is predicted, therefore, that this difference of reproductive behavior in two *Mazus* species affects their population dynamics. These dynamics in the sympatric habitats, the rice paddy fields, appear to hold the key to the solution of the following problem; annual species are better colonizers than perennial ones in disturbed habitats as they produce many seeds reliably by self-pollination and establish new populations rapidly (Baker 1955, 1959; Stebbins 1957, 1958; Antonovics 1968; Lefėbvre 1970; Jain 1976).

The results give a model of the population dynamics. Four stages can be illustrated: 1) rice cropping; on the levee, there were about 3 plants of *M. japonicus*/m^2 and about 100 plants of *M. miquelii*/m^2. In the non-cultivated paddy field, there were about 3 plants of *M. japonicus*/m^2 only in winter. 2) non-cropping (relinquishment); *M. japonicus* colonized into the abandoned paddy field by seeds. On the contrary, *M. miquelii* invaded from the levee to the abandoned paddy field by stolons. 3) ill-drained abandoned paddy field; *M. japonicus* decreased (about 50 plants/m^2 in the center) and *M. miquelii* increased by stolons (about 350 plants/m^2 near the levee). This pattern may be presumed by the density of two species in the parts near the creek. 4) well-drained abandoned paddy field; *M. japonicus* increased by seeds (about 350 plants/m^2 in the center) and *M. miquelii* decreased (a few/m^2 even near the levee).

The population dynamics in the two *Mazus* species seemed to be dependent on the competition among other species, their seed germination, and the rooting (ramet formation) from node of stolon in *M. miquelii.* The number of species on the levee was twice as many as in the fallow paddy field. Therefore, on the levee the density of two *Mazus* species might be difficult to increase by seeds, because those which light germinators could hardly germinate in the shade of other plants, or even if germination was possible, their seedlings may have soon died. However, *M. miquelii* could reproduce on the levee by stolons.

As grasses were dominant on the abandoned levee, there were only 29 plants of *M. miquelii*/m^2. Moreover, there were 108 plants of *M. japonicus*/m^2 in the abandoned paddy field, for annual weeds were dominant here.

By comparison with the seed germination of two *Mazus* species, M. japonicas was able to germinate better under several temperature and under lower soil moisture conditions than was *M. miquelii*. However, the seed germination of *M. japonicus* occurred more rapidly than that of *M. miquelii*. The rooting from the node of stolon in *M. miquelii* required less soil moisture (34.4%) than the seed germination (79.1%). Consequently, *M. japonicus* was a better colonizer than *M. miquelii* in disturbed habitats. There was an abundance of plants of *M. miquelii* only on the levee, a relatively stable habitat.

In the winter plants of *M. japonicus* the first flowered capsule seeds were germinating more rapidly than the 4th and 8th. On the contrary, in summer plants the 8th flowered capsule seeds were germinating more rapidly than the 1st and 4th. Specifically, it appeared that the germination requirements differ widely among seeds. This fact may be related to the vigorous germination in May-July and the variety of seed germination.

Life history strategy of two *Mazus* species

The schematic model of the life history of *M. japonicus* and *M. miquelii* is shown in Fig. 11.

M. japonicus is an year-long annual and self-pollinated species. This species reproduces by numerous seeds and grows on upland fields, roadsides, and so on. There is the first main period of seed germination in April-June. The summer population is composed of the seedlings which are grow from the seeds of winter plants or the buried ones. These seedlings grow rapidly in summer and then flower, fruit, and disperse numerous seeds in June-October. There is the second main period of seed germination in September-October. The winter population is composed of the seedlings which are grown from the seeds of summer plants or the buried ones. These seedlings grow leisurely in winter and then flower, fruit and disperse numerous seeds in April-June.

As the germination of *M. japonicus* was not homogeneous, the age diversity was very high in a garden population. Plant height, the number of leaves and the number of inflorescences had specially high diversity (c.v.). The length and width of the largest rosette leaf had rather low diversity. In summer large plants flowered and had died by November. However, a part of small seedlings might probably become large plants and then flower in next spring.

M. miquelii is a perennial and cross-pollinated species. This species reproduces mainly stolons and grow only on the levees of rice paddy fields. The wintered rosette plants flower, fruit and disperse many seeds in April-June. Moreover, they form many ramets by stolon vegetatively in May-October. Their ramets grow in autumn-winter and flower in the next spring. The seeds and buried ones germinate in May-June. These seedlings grow in summer, and then flower, fruit and disperse a few seeds in August-October. Similarly, they form some ramets by stolon in September-October. Their ramets grow in winter and flower in the next spring.

Compared with the seasonal change and percentage allocation of total dry weight throughout the life history of the summer population in *M. japonicus*, those of the winter population were characterized by the following three features; 1) the crude reproductive efficiency of the winter plant was rather lower than that of the summer one, 2) the winter plant stored a lot of substance in the roots during winter, but not the summer one, 3) at the end of growing period the dry weight of a winter plant was about three times as much as that of summer one. In short, the summer plant produced many seeds continuously with the storage of a little substance in roots, but the winter plant stored a lot of substance in roots during winter and began to produce many seeds in spring. This fact showed the difference between the life history of the summer plant and that of winter one in *M. japonicus*.

The mother plant of *M. miquelii* developed many roots and contributed to the elongation of stolons in May or September. The daughter plant (ramet) stored a lot of substance in roots during winter, and began to produce many seeds and new ramets by stolons in spring. On the other hand, the plant formed by seed hardly produced seeds, but did ca. 10 ramets in autumn. In the next spring these ramets flowered and produced many seeds and ramets by stolons. However, few plants formed by seed were observed in natural populations. These plants, therefore, could play only a secondary role in the life history strategy of *M. miquelii* two years after germination except that the genetic variability resulted from outcrossing would increase in their population.

The winter plant of *M. japonicus* and the daughter plant (ramet) of *M. miquelii* had such a character as stored much substance in roots during winter in common with each other. Moreover, all species of genus *Mazus* except *M. japonicus* are perennial ones which grow in winter and flower in spring-early summer (Peking Institute of Botany 1975). *M. japonicus,* therefore, might have been winter annual and then became a year-long one by the decrease of the seed dormancy and the early maturity from which the adaptation to the disturbed habitats resulted.

These series of studies in *Mazus* (Kimata 1978, 1979, 1986, 1991) might give a clue to the solution of problems on the life history strategy proposed by Harper (1967), Kawano (1975) and so on, i.e., concerning the longevity and expression of the life cycle, the program of energy allocation to reproduction and the number of seeds or vegetative propagules produced. *M. japonicus* is a self-pollinated annual species, while *M. miquelii* is a cross-pollinated perennial one. The former is a wonderful colonizer and invades into the disturbed habitats. The clear differences of population dynamics in the sympatric habitat between *M. japonicus* and *M. miquelii* may indicate each characteristic in their reproductive strategy. Between annual species and perennial species there are the conspicuous differences of life history strategy which consists of the above ecological characteristics. These differences may have resulted from the adaptation to the environment of their habitats (Figure 5).

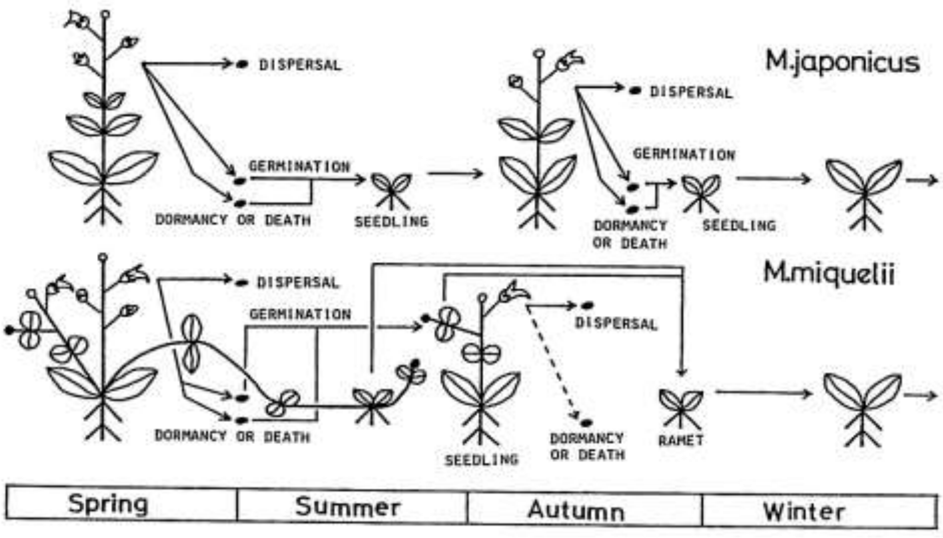


Figure 5. Schematic model of the life histories of *M. japonicus* and *M. miquelii*
⬬ seed; ○flower bud; ●shoot apex.

These experimental data on the life history strategies of two *Mazus* species could provide some further evidences for the evolutionary trend from cross-pollinated perennials to self-pollinated annuals in the flowering plants as a whole.

Comparison of reproductive systems in five species and subspecies of genus *Cardamine*, Cruciferae

The reproductive systems of *Cardamine flexuosa* ssp. *flexuosa* and ssp. *fallax, C. impatiens* (annuals), *C. scutata* and *C. lyrata* (perennials), were compared, in order to provide further evidence for the evolutionary trend from cross-pollinated perennials to self-pollinated annuals. Moreover, this study was devoted to obtain some information concerned with the intraspecific differentiation of a year-long annual type from a winter annual type in *C. flexuosa* (Kimata 1983).

Seven strains of *Cardamine flexuosa* ssp. *flexuosa* With. were collected mostly at fallow paddy fields in Tokyo, Kanagawa, Saitama, Chiba, Shizuoka and Kyoto Prefectures. Two strains of *C. flexuosa* ssp. *fallax* O. E. Schulz were collected at shady gardens in Tokyo. *C. impatiens* L. was collected at a forest floor of *Cryptmeria japonica* D. Don in Yamanashi Prefecture. Five strains of *C. scutata* Thunb. were collected mostly at creeks in Tokyo, Shizuoka and Kyoto Prefectures. Two strains of *C. lyrata* Bunge were found at paddy fields in Aichi and Mie Prefectures (Figures 6 and 7). More than 20 plants were collected in each strain, while, 10 plants were examined, and the remaining plants were placed on file with the Herbarium of Tokyo Gakugei University.

C. flexuosa and *C. impatiens* are self-pollinated annual species, *C. sucutata* is a cross-pollinated perennial species, and *C. lyrata* is a cross-pollinated perennial species with self-incompatibility. The perennial species may be either cross- or self-fertilized depending on the species. The evolutionary trend of breeding system may progress from cross-pollinated perennial with self-incompatibility to self-pollinated annual via self-pollinated perennial without self-incompatibility. Also, the above trend is shown clearly in the present four species of genus *Cardamine*.

Figure 6. *Cardamine flexuosa*
a, in paddy field; b, shady garden; c, on rock fence;
d, artificial hybrid F1 between two subspecies.

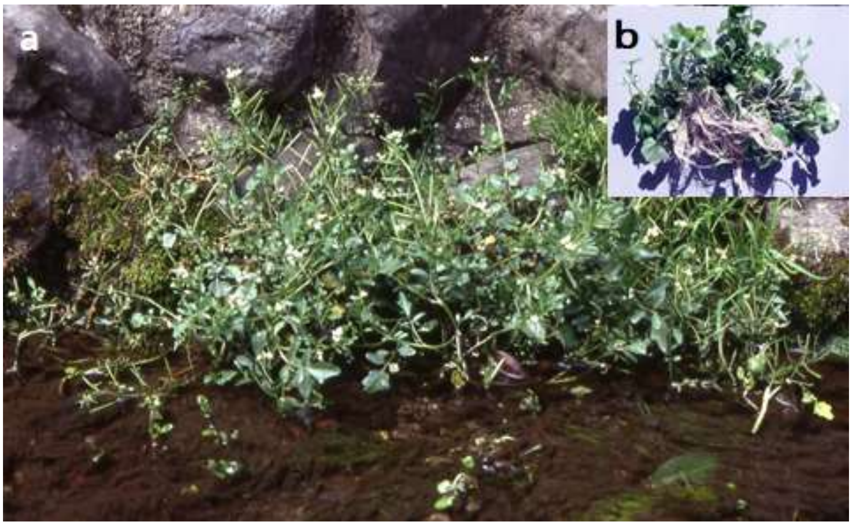


Figure 7. *Cardamine sucutata* in stream
a, flowering; b, rosette

The self-pollinated annual species are usually better colonizers in disturbed habitats, because massive seed production in the early stage of colonizing process plays an important role in the establishment of new populations (Stebbins 1958; Ehrendorfer 1965; Antonovics 1968; Lefèbvre 1970). Two subspecies of *C. flexuosa* well adapt to disturbed habitats. *C. flexuosa* ssp. *flexuosa* flowers in February-April and produces a great deal of small seeds which fall near its own stump in paddy fields. The seeds are dispersed uniformly during the cultivation practice in the fields. They are kept there in dormant condition until autumn. On the other hand, *C. flexuosa* ssp. *fallax* flowers in February-April and in June-November. Many seeds produced, fallen evenly within a distance, and germinate in May-October after a short dormant period and establish summer and winter populations. Therefore, *C. flexuosa* ssp. *flexuosa* and *C. flexuosa* ssp. *fallax* may have different seed dispersal strategy. Friedman and Stein (1980) reported that the annual *Anastatica hierochuntica*, Cruciferae has two contrasting dispersal strategies (dispersal on the spot and to a distance) which are dependent upon the balance between rainfall and runoff. *C. impatiens* is a self-pollinated annual species but it has adapted to rather stable habitats such as muddy floor and margin of forests. C. impatiens in March-May and produces a great deal of small seeds which fall at a limited distance by the erect growth form. Watkinson (1978) reported that the dispersal distance strongly correlated with the height of the infructescence in a winter annual grass, *Vulpia fasciculate*. Actually, seeds of *C. impatiens* with tall infructescence are dispersed farther than seeds of *C. flexuosa* and *C. scutata* with low infructescence. Seed germination of *C. impatiens* occurs in August after short seed dormancy. *C. scutata* and *C. lyrata* have adapted well to the paddy field which is cultivated regularly, supplied much fertilizer, and muddy throughout the year. *C. scutata* flowers in February-April and August-September, and produces rather many seeds which fall evenly into water of creek within a distance. The seeds without dormancy germinate in May. *C. lyrata* flowers in May and produces a few seeds which fall down to water and they may be dispersed by floating (Figure 8). They germinate in autumn after a long dormancy. These results well indicate that the better colonizing species adapting to grow in the disturbed habitats are installed more efficient seed dispersal mechanism.

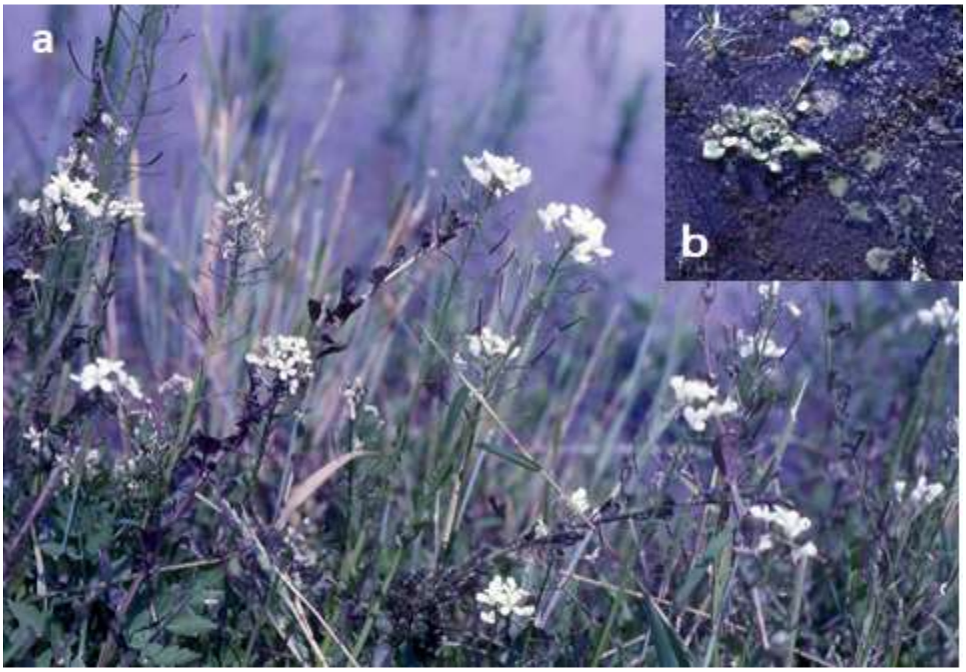


Figure 8. Cardamine lyrate in paddy field

a, flowering; b, ramets

The reproductive allocation of dry matter into sexual structures (e.g., seed) is considerably higher in annuals than in perennials. On the contrary, in perennials allocation into asexual structures (e.g., vegetative propagules and storage organs) is often very high (Harper 1967; Harper and Ogden 1970; Kawano 1974, 1975). In the present study a self-pollinated annual *C. flexuosa* allocates 26% of total dry matter into the siliques (a sexual structure). However, a self-pollinated perennial *C. sucutata* allocates only 12% of total dry matter into siliques and 48% into ramets (an asexual structure) at the end of growing season. A cross-pollinated perennial *C. lyrata* allocates less than 1% into siliques but 80% into stolons. Bell et al. (1979) determined the seasonal changes of biomass allocation in eight winter annual species. They described that 12-22% of total biomass locates in the roots until late flowering period when root allocation declined, and that maximum investment in reproductive structures attains 16-50% of total biomass. A winter annual *C. flexuosa* showed similar percentage allocation into roots and siliques.

The rooting ability of stem segment is higher in *C. lyrata* (75.0%) than in *C. flexuosa* ssp. *flexuosa* (17.5%) or *C. flexuosa* ssp. *fallax* (57.5%). However, it is very low (5.0%) in *C. scutata.* The weak rooting ability in *C. scutata* may closely relate to a low degree of vegetative reproduction. *C. lyrata* produces ramets about 27 times as many as *C. scutate* (Table 6).

Table 6. Vegetative propagation of genus *Cardamine*

Species	No. of plants	No. of vegetative propagules	
		Range	Average
Cardumine sucutata	20	1～12	4.6
Cardumine lyrata	8	87～167	133.3

These species of the genus *Cardamine* used in the present study are distinguished easily by several morphological characters. Among them the corolla of *C. lyrata* is about three times as large as that of other species. The larger corolla of this species may relate closely with its cross-pollination system.

In spite of complete intraspecific cross-ability, the subspecies differentiation of *C. flexuosa* occurs in several morphological and other characters, such as growing season, seed dispersal mode, germination period, flowering period, and so on, as shown in Table 7. *C, flexuosa* ssp. *flexuosa* can establish large population only in the restricted habitat, fallow paddy fields. On the other hand, *C. flexuosa* ssp. *fallax* can establish merely small population (a few per m^2) in spite of growing in the various habitats, i.e., gardens, roadsides and nurseries, because the present subspecies produces fewer seeds than the former subspecies and can establish only in rather wet microenvironments.

Table 7. Summary on reproductive system of genus *Cardamine*

Species	Spring	Flowering season	Summer	Autamun	Winter	Growth habit
Cardamine flexuosa	rosette, bolting	winter form flowering, self-pollination, fructfication, dead		germination	rosette	winter annual + year long annual
			germination, growth in summer,	summer form flowering/fructfication	dead	
Cardamine flexuosa ssp. fallax	rosette, bolting	flowering and fructfication, self-pollination, dead		seed germination	rosette	winter annual
Cardamine impatiens	rosette, bolting	flowering and fructfication, self-pollination, dead		seed germination	rosette	winter annual
Cardamine scutata	rosette, bolting	flowering and fructfication. self-pollination, self-compatible	vegetative propagation, seed germination		rosette	perennial
Cadamine lyrata	rosette, bolting	flowering and fructfication. cross-pollination, self-incompatible	vegetative propagation by stolons		ramets, rosette	perennial

As discussed above, the annual growth habit is classified into three different types; summer annual, winter annual and year-long annual. *C. flexuosa* ssp. *flexuosa* is a winter annual subspecies, and ssp. *fallax* a year-long one as being able to establish a summer population. Generally, the genus *Cardamine* grows in winter and flowers in spring. The year-long annual growth habit of *C. flexuosa* ssp. *fallax* might be derived from winter annual.

In the present study, the experimental data and observations on the life history strategies of the genus *Cardamine* provide some further evidences for the general evolutionary trend from cross-pollinated perennial to self-pollinated annual breeding system in flowering plants.

Intraspecific differentiation of C. *flexuosa* in Japan and Nepal

The term "ecotype" was proposed for the ecological sub-unit of the product arising as a result of the genotypical response of an ecospecies to a particular habitat (Turesson 1922, 1925). The ecotype is a basic biological entity. Its entity is adjusted to a range of habitats characterized by particular environments, e.g., annual fluctuations in climate, soil, other organisms and so on. The ecotypic differentiation is essentially physiologic-genetic (Clausen 1967; Armbruster 1985).

In widespread species, the ecogeographical differentiation is closely related to the size, migration, variation, selection, reproduction and isolation of populations (Ehrendorfer 1968; Barton and Charlesworth 1984). There are two extreme types of intraspecific differentiation: allopatric and partly sympatric patterns. The former pattern is found most typically in allogamous groups without restriction on intrapopulation gene flow, while the latter and more complex patterns are found in groups where intrapopulation gene flow is restricted (Ehrendorfer 1968; Kawano et al. 1971; Kawano 1974). The term “sympatric” differentiation has not been used to include such cases of differentiation on adjacent populations that are allopatric on the geographical criteria. Those adjacent populations are, therefore, described as parapatric (Jain and Bradshaw 1966).

The intraspecific differentiation of *C. flexuosa*, a widespread weed collected in Japan and Nepal, was compared morphologically, ecologically and genetically. It is interesting to compare the intraspecific differentiations occurring in Japan (the eastern border of Sino-Japanese Region) and in Nepal (near the western border of the Region).

In the present study six biotypes growing parapatrically in paddy fields, gardens and a stone wall in Japan and Nepal were detected (Kimata and Kobayashi 1996). Seventeen strains of *C. flexuosa* were used in the present study. Japanese strains were collected from five habitats: a garden, a stone wall, a roadside, a ditch and fallow paddy fields in three locations, Tokyo. Nepalese strains were collected from three habitats: a garden in a mountain area (Syangboche, about 4,000m alt.), two gardens, one in Ratna Park and another at a hotel, and a paddy field (Katmandu, about 1,300m alt.). These plant specimens were placed on file with the Herbarium of Tokyo Gakugei University.

Considerable differences in the intraspecific cross-ability observed among different combinations of biotypes indicate the occurrence of intraspecific differentiation among Japanese *C. flexuosa* strains. The intraspecific differentiation has already been suggested by several morphological and ecological characters, such as growing season, mode of seed dispersal, germination period, flowering period and others (Kimata 1983). The winter annual paddy field biotype can establish large populations only in the restricted habitats, such as the winter fallow paddy fields. On the other hand, the year-long annual garden biotype, which produces fewer seeds can establish small populations (a few plants per m^2) in rather wet microenvironments of various habitats, such as gardens, roadside and nurseries. Their F_1 hybrid has intermediate characters between the paddy field biotype and the garden biotype in Japan. Site 7 (a large population) is a parapatric habitat for both biotypes, and the plants growing here show wide variation in morphological and ecological characters, which suggests the occurrence of hybridization between these two biotypes.

Various patterns of phenotypic segregation of the six quantitative characters of Japanese F_2 hybrids and a comparison of ten characters between the paddy field biotype and the garden biotype clearly indicate the occurrence of intraspecific differentiation in *C. flexuosa*. The plant height of paddy field biotypes is taller than that of garden biotypes both in Japan and Nepal. However, on the six other characters (number of tillers, silique length, width of terminal leaflet, stem color, hairiness of stem and plant form), the variation patterns of Japanese biotypes show the opposite trend to those of Nepalese biotypes. Therefore, the intraspecific differentiation of *C. flexuosa* in Japan did not occur in parallel with that in Nepal.

The intraspecific differentiation of *C. flexuosa* has occurred in many directions. According to the cross ability among strains examined, the garden biotype is shown to be isolated sexually from the stone wall biotype, but not from the paddy field biotype in Japan. The garden biotype is considered to be isolated sexually from the paddy field biotype in Nepal because of the necrosis of F_1 hybrid seedlings. As F_1 hybrid seedlings become necrosis, the Japanese paddy field biotype is also considered to be isolated from the Nepalese paddy field biotype. As the other hand, the Japanese garden biotype is not considered to be isolated from the Nepalese garden biotype, which itself has not been isolated from the mountain biotype. As the results of crossings between the Japanese paddy field biotype and the Nepalese paddy field biotype, occurrence of sexual isolation among them is also indicated. The Japanese paddy field biotype is not very isolated, yet, from the Nepalese mountain biotype. Therefore, each garden biotype in Japan and Nepal is the prototype among six biotypes and can be called a garden "ecotype." Turesson (1922, 1925) defined the term "ecotype" as the product of the genotypical reaction of ecospecies to a particular, defined set of environment conditions. He also defined the sub-taxon "ecophene" as the reaction-type to a unique microenvironment.

Cross ability among six strains of *C. flexuosa* from Japan and Nepal, and the seed germination rate and pollen fertility of F_1 hybrids.

Within a limited comparison of Japan and Nepal carried out in the present study, a model of intraspecific differentiation of *C. flexuosa*. The garden ecotype may be an original biotype because neither garden biotype is isolated for from the other. It is very interesting fact that there is no sexual isolation between the garden ecotype and the paddy field ecophene in Japan, but not between the garden ecotype and the paddy field ecotype in Nepal. As observed in other weeds growing in paddy fields (Sakamoto 1961; Matsumura 1967; Linhart 1974), the Japanese paddy field ecophene of *C. flexuosa* shows some phenotypic variation in various characters. This fact indicates a great diversity of intraspecific differentiation in *C. flexuosa* which may correlate with the period when rice cropping in paddy fields dispersed throughout Asia. The stone wall ecotype (83011) growing on a stone wall in Koganei, Tokyo is different morphologically, ecologically and genetically from the garden ecotype (83010). The Nepalese garden ecotype includes the mountain ecophene in Nepal. The intraspecific or ecotypic differentiation has occurred independently in Japan and Nepal. The intraspecific differentiation of *C. flexuosa* in the process adaptation to gardens, paddy fields stone wall and so on has occurred independently in Japan and Nepal. A model of intraspecific differentiation of *C. flexuosa* is proposed within a limited comparison in Japan and Nepal.

Comparative Studies on the Reproductive Systems of *Rorippa cantoniensis, R. islandica, R. dubia, R. indica* and *R. x brachyceras*, Cruciferae

The objective of this study on genus *Rorippa* was to make clear the life cycle and adaptive strategy by ecological genetics or evolutional biology. Mainly, it was the characteristics of a natural hybrid, *R. x brachyceras* (perennial, sterile) between *R. islandica* (annual) and *R. indica* (perennial).

Genus *Rorippa*, Cruciferae had dispersed 50 species in the world and 5 species in Japan. *R.*

islandica (Oeder) Boras grows in riverside, wetland, levee of paddy field, wheat field, orchard and so on in the warm temperate zoon from Hokkaido to Kyushu, Japan, and Canada, Australia, New Zealand. *R. indica* (L.) Hiern grows in field, levee, roadside, garden, etc., from Japan, Formosa, China, Korea, Malysia, to India. *R. cantoniensis* (Lour) Ohwi grows in riverside, wheat field, levee from Central Japan to South Korea, China, and Amur. *R. dubia* Hara grows in semi-shade place from Central Japan to South East Asia, South/North America. *R. x brachyceras* have been collected from some places in Japan. *R. sylvestris* (L) Besser have been collected from some sites of Hokkaido and Sugadaira, Ngano in Japan, and then from Finland, Denmark, Switzerland, Netherland, Canada, USA, and so on. *R. austriaca* (Crantz) Besser have collected at Sakura, Chiba (Victorin 1930, Jhon Wiley & Sons. Inc. 1979, etc.).

R. cantoniensis and *R. islandica* are considered to be self-pollinated annual species and *R. dubia* and *R. indica*, self-pollinated perennial species. *R. x brachyceras* seems to be a hybrid between *R. islandica* and *R. indica* (Kitamura, 19). This natural hybrid and artificial hybrids sterile perennial plants. One strain of *R. sylvestris* grown in Nagano is a cross-pollinated perennial, but another grown in Hokkaido is a sterile perennial (Nakatani and Kimata, 1993).

Stebbins (1950, 1957, 1958) recognized that annual species are predominantly self-fertilized in spite of the great diversity in the reproductive systems, while perennials are cross-fertilized in Gramineae and Compositae. This trend may be generally admitted, including the cases of *Mazus*, Scrophurareaceae (Kimata, 1978), and *Cardamine*, Cruciferae (Kimata, 1983; Kimata and Kobayashi, 1996). However, there are many exceptions and compromised systems such as the case of *Rorippa*, Cruciferae, in the present study. The self-pollinated annual species are often the best colonizers in disturbed habitats, because massive seed production in the early stage of the colonizing process plays an important role in the establishment of new populations (Stebbins, 1958; Ehrendorfer, 1965; Antnovics, 1968; Lefebvre, 1970).

In this case, of course, *R. cantoniensis* and *R. islandica* are excellent annual colonizers by means of numerous small seeds, and also two self-pollinated perennials of *R. dubia* and *R. indica* are better colonizers with large seed production. *R. dubia* and *R. indica* have not only certain possibilities of vegetative propagation by means of root segments but also hopeful possibilities by stem segments, when they are cut for physical weeding in shady gardens and roadsides. *R. x brachyceras* and F_1 hybrids can maintain themselves with the perenniality and vegetative reproduction, in spite of their sterility. Even if *R. islandica* is an annual species, it has large potentiality of vegetative reproduction in a moist field as cutting it for weeding at the juvenile stage. Moreover, *R. sylvestris* is cross-pollinated or sterile perennial species but a better colonizer too with vigorous vegetative reproduction (Figure 9), Nakatani and Kimata, 1993).

Figure 9. Weeds of genus *Rorippa*

a, *R. islandica*; b, *R. dubia*; c, *R. cantoniensis*; d, *R. sylvestris*; e, *R. indica*.

R. islandica and *R. indica* seem to cross easily each other in sympatric populations such as paddy fields (Figure 1) and make an interspecific hybrid, *R. x brachyceras*, because their artificial cross-abilities are often very high and F1 hybrids resemble *R. x brachyceras* in the morphological and ecogenetical characteristics. The F_1 hybrid of *R. indica* x *R. islandica* shows a heterosis of vigorous growth with high seed germination rate and maintains itself with perenniality and vegetative reproduction (Kimata and Shibata, unpublished). On the contrary, the reciprocal F_1 hybrid shows weak growth with low seed germination rate. Both F_1 hybrids do not produce any seeds at least through the pollen sterility and F_2 hybrids never grow. *R. islandica* and *R. indica* have same chromosome number, 2n= 16 and 8 bivalents in meiosis, while *R. x brachyceras* and their F_1 hybrids have 16 monovalents. Both species differ in their cytological genomes. *R. islandica* has already reported the chromosome number, 2n = 16 (2x) and 32 (4x) (hybridization).

The B_1 and B_2 hybrids show well growth when the F_1 of *R. indica* x *R. islandica* and then its B_1 were repeatedly backcrossed by *R. indica*. The introgression between *R. islandica* and *R. indica* seems to be possible theoretically, but it has not been observed in natural populations yet. These Japanese interspecific F_1 hybrids do not accept any pollens of *R. islandica*, but Nepalese interspecific F_1 hybrids accept the pollens of both *R. islandica* and *R. indica*. Therefore, it seems to be more or less possible that the introgressive hybridization occurs in natural populations of Nepal. Additionally, *R. islandica* does not make a sexual barrier between Japanese strain and Nepalese, while *R. indica* has made a sexual barrier each other.

R. islandica is an annual, while *R. indica* is a strict perennial. *R. x brachyceras* and most of their interspecific F1 hybrids are perennials. These facts indicate clearly that perenniality is a dominant against annuality. However, two F_1 hybrids derived from Japanese *R. islandica* as a female strain show rather weaker perenniality. It needs more detail investigation that the intraspecific F_1

hybrid between Japanese strain and Nepalese of *R. islandica* shows weak perenniality too. This trait may be concerned with the potentiality of vegetative reproduction in *R. islandica* at the juvenile stage.

R. indica has more attractive nectar contents and bigger yellow flowers for pollinators such as bees than *R. islandica*. The pollinators ensure their feed by much volume and high quality of the nectar and the even a little bigger yellow flower is a good sign for inducing pollinators to out-cross in *R. indica* such as out-crossed perennial. The other self-pollinated species do not need to make them. Actually, *R. indica* gets more visits from pollinators than *R. islandica*, and also does the second visit after pollinators visit first *R. islandica*. Moreover, *R. x brachyceras* is always growing around plants of *R. indica* in natural populations. The similar hybridization of genus *Rorippa* has often been observed in Europe (Howard, 1947; Mulligan and Porsild, 1968). It comes to the conclusion that most plants of *R. x brachyceras* are F_1 hybrid plants derived from *R. indica* x *R. islandica*.

R. indica has more attractive nectar contained a large quantity of sugars and amino acids and bigger yellow flowers for pollinators and gets more visits from them than *R. islandica*. *R. islandica* ($2n = 16$) and *R. indica* ($2n = 32$) cross easily each other in natural habitats and make their interspecific hybrids. Artificial F_1 hybrid ($2X = 24$) of *R. indica* x *R. islandica* resembles *R. x brachyceras* ($2X = 24$) in the morphological and ecogenetical characteristics. These hybrids are sterile perennials but show a heterosis growing well and maintain themselves with vegetative reproduction. Therefore, *R. x brachyceras* is derived from the F_1 hybrid of *R. indica x R. islandica*. The self-pollination rate, calculated from the bagged inflorescences of *R. cantoniensis, R. islandica, R. dubia* and *R. indica* was 98.1-100 % as shown in Table 4. The pollen fertility of these four species was 87.4-96.2 %, but that of *R. x brachyceras* was only 2.5 % as shown in Table 5. The fructification rate of four species, assessed from open-pollinated inflorescences, was 95.3-100 %, but that of *R. x brachyceras* was nil. These data indicate that *R. cantoniensis, R. islandica, R. dubia* and *R. indica* are all self-pollinated species. However, only *R. x brachyceras* is sterile. The petal length was around 1 mm in *R. cantoniensis* and *R. islandica*, ca. 2.2 mm in *R. x brachyceras* and 3.5 mm in *R. indica*. *R. dubia* had not any petal, but attached one or two petals at an irregular case. Usually, these species have four yellow petals.

The number of siliques per plant was ca. 380 in *R. cantoniensis*, 690 in *R. islandica*, 230 in *R. dubia*, 130 in *R. indica* and 1050 in *R. x brachyceras*, respectively as shown in Table 8. The number of seeds per silique was ca. 206 in *R. cantoniensis*, 45.8 in *R. islandica*, 74.0 in *R. dubia*, 79.3 in *R. indica* and nil in *R. x brachyceras*, respectively. A plant of *R. cantoniensis* produced ca. 77,900 seeds by means of many tillers. A plant of *R. islandica* produced ca. 30,000 seeds. A plant of *R. dubia* produced ca. 16,000 seeds. A plant of *R. indica* produced ca. 9,600 seeds, with a few main inflorescences by a few tillers. On the other hand, a plant of *R. cantniensis* produced ca. 77,000. Of course, *R. x brachyceras* did not produce any seeds. The seed weight of *R. indica* (64.1 mg/1,000 seeds) was almost the same weight of *R. dubia* (61.5 mg/1,000 seeds), a little heavier than that of *R. islandica* (50.9 mg/1,000 seeds), and two and half times that of *R. cantoniensis* (26.8 mg/1,000 seeds).

Table 8. Fructification rate from open pollination and seed production in genus *Rorippa*

	R. cantoniensis	***R. islandica***	***R. dubia***	***R. indica***	***R. x brachyceras***
Fructification rate (%)	100	95.3	95.8	96.3	0
Pollen fertility (%)	87.4	92	94.3	96.2	2.5
Siliques per plant	377.8	686.5	227.1	126	1051.7
Seeds per silique	205.7	45.8	74	79.3	0
1,000 seeds weight (mg)	26.8	50.9	61.5	64.1	-
Seeds per plant 1)	77,714	29,964	16,100	9,622	0

1) Seeds per plant = Siliques per plant x Seeds per silique x Fructification rate

Figure 10. *R. sylvestris* (a) and the sprouting from roots (b) in Hokkaido

The reproductive systems of *Rorippa cantoniensis, R. islandica, R. dubia,* R. x brachyceras (a natural hybrid) and an artificial hybrid between *R. indica* and *R. islandica* were compared. *R. cantoniensis* and *R. islandica* are self-pollinated annuals, while *R. dubia* and *R. indica* are self-pollinated perennials. These four species produce a great many seeds, but the both perennial hybrids do not produce any seeds because of the sterility. *R. islandica*, *R. dubia*, *R. indica* and two hybrids have large potencialities of vegetative reproduction by means of root and stem segments. *R. indica* and *R. islandica* may cross each other and make an interspecific hybrid, *R. x brachyceras*. The reproductive systems of weedy *Rorippa* species may indicated each characteristic in the colonizing strategy into their habitats (Figure 10, Figure 11, Figure 12).

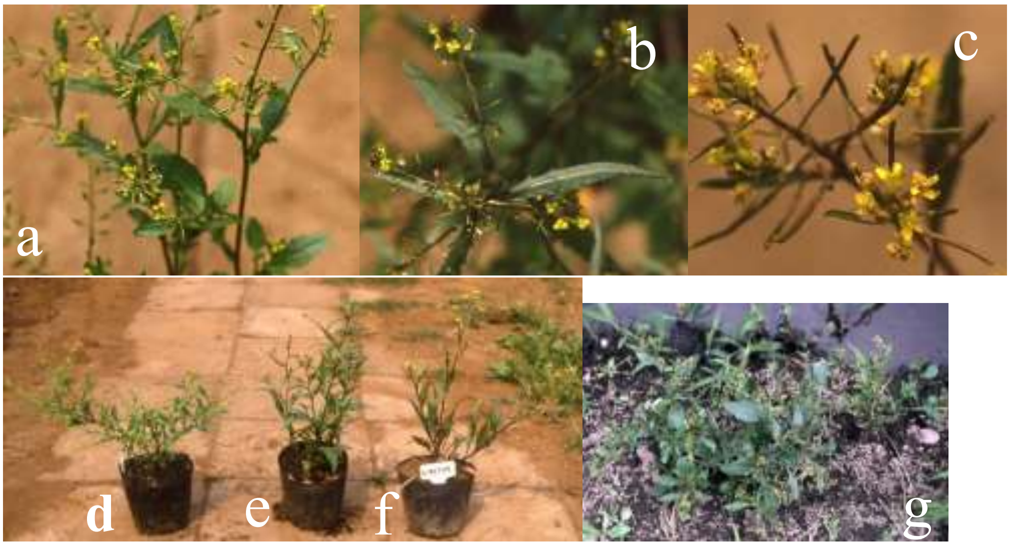


Figure 11. ***R. x brachyceras*****: an artificial hybrid between *R. islandica* and *R. indica***

a, *R. islandica* (annual); b, a hybrid F_1 (perennial, sterile); c, *R. indica* (perennial);

d, *R. islandica*; e, F_1 hybrid; f, *R. indica*; g, natural hybrid *R. x brachyceras* (perennial, sterile).

R. cantoniensis is a winter annual grown mainly in fallow paddy fields, while *R. islandica* is a year-long annual not only grown in and around paddy fields but also colonized aggressively into moist upland fields. *R. dubia* is a perennial grown in gardens and along roadsides, while *R. indica* is a perennial not only grown in gardens and along roadsides but also colonized aggressively into upland and paddy fields. *R. cantoniensis* and *R. dubia* germinated in autumn and flowered in the next spring. On the one hand, *R. islandica* and *R. indica* germinated twice mainly in autumn and in the next early summer after its fruiting. *R. islandica* flowered twice mainly in April-May and seldom in July-August. Also, *R. indica* flowered twice mainly in May-June and sometimes in August-September. *R. islandica* often grows together with *R. indica* in and around paddy fields (Table 9). These two species may cross each other during the flowering period overlapped in May and make an interspecific hybrid plant, *R. x brachyceras*. This hybrid plant is a sterile perennial but maintains itself by means of vegetative reproduction. The reproductive systems of weedy *Rorippa* species may indicate each characteristic in the colonizing strategy into their habitats.

Table 9. Life cycle of weedy *Rorippa* species

Species	Sprinng	Flowering season	Summer	Autamun	Winter	Growth habit
R. islandica	rosette, bolting	flowering, fructification		gernination	rozett	yearlong annual
Cold region		germination, growing, flowering, fructification				summer annual
R. indica	rosette, bolting	flowering, fructification, dormancy		germination, budding	rozett	perennial
R. x brachyceras	rosette, bolting	flowering, sterile	stock dormancy	budding	rozett	perennial
R. cantoniensis	rosette, bolting	flowering, fructification, dormancy		germination	rozett	winter annual
R. sylvestris	rosette, bolting	flowering, fructification, dormancy		germination, budding	rozett	perennial
Hokkaido	rosette, bolting	flowering (sterile)	dormancy, budding from stock and roots		rozett	perennial

The natural habitats of *R. cantoniensis* and *R. islandica* are restricted mostly to fallow paddy fields and levees but sometimes the latter invades into upland fields. *R. dubia* grows in shady gardens, along roadsides and levees of upland field. The habitat of *R. indica* is found widely in levees of paddy and upland fields, gardens and along roadsides. Moreover, this species often invades into paddy fields and upland fields. *R. x brachyceras* is found in paddy fields and levees sometimes. *R. cantoniensis, R. islandica* and *R. indica* grow sympatrically in fallow paddy fields, while *R. dubia* grows in a garden together with *R. indica*. *R. cantoniensis* was a winter annual observed only from autumn to next spring. *R. islandica* was a year-long annual observed in both winter and summer, but the summer population was small on the levees of paddy field in Tokyo. *R. dubia* and *R. indica* were observed in all seasons.

The stems of *R. cantoniensis, R. islandica, R. dubia, R. indica* and a F1 hybrid were cut into about 10 mm length and 2-mm diameter segments, each with one leaf. Also, their roots were cut into about 10 mm length and 3-mm diameter segments. The cuttings (over 28 segments per species) were grown on wet papers in Petri dish under 23 C constant and about 1,000 lux continuous light. After two weeks, the rooting from stem segments and the sprouting from root segments were observed.

The rooting rate from stem segments and the sprouting rate from root segments of *R. cantoniensis* were both nil. The rooting rate from stem segments was 52.4 % in *R. islandica*, 16.0 % in *R. dubia*, 8.5 % in *R. indica* and 50.0 % in F1 hybrid between *R. indica* and *R. islandica*. These stem segments showed well shooting rates ranging from 54.9 % to 91.2 % and vigorous growth too. The sprouting rate from root segments was 78.0 % in *R. islandica*, 91.2 % in *R. dubia*, 99.4 % in R. indica and 100 % in F_1 hybrid between *R. indica* and *R. islandica*. Those shoots of root segments grew vigorously and showed well rooting rates ranging from 62.0 % to 100 %. These data clearly indicate that *R. cantoniensis* does not propagate with any vegetative reproduction, while the others have large potentiality of vegetative reproduction by means of root segments (Table 10). Moreover, *R. islandica* and F1 hybrid between *R. indica* and *R. islandica* may also propagate with rooting and shooting from stem segments, when they are cut for weeding in a moist fallow paddy field.

Table 10. Sprouting from buds and stem segments of genus *Rorippa*

	R. islandica		***R. indica***		**Artifitial F_1**	***R. dubia***	***R. cantniensis***
No. of root segments	44	106	59	101	113	34	28
No. of sprouting segments	2.9	2.1	4.1	2.4	3.3	3.9	0
The longest bud mm	9.0	5.4	22.7	25.5	30.4	7.7	0
Sprouting %	68.2	82.1	100	99.0	100	91.2	0
Greening %	61.3	73.6	100	99.0	100	82.4	0
Rooting %	70.5	58.5	100	95.0	100	91.2	0
No. of stem sections	42	105	45	108	96	75	30
No. of roots	5.2	0.8	0.1	0.1	1.1	0.3	0
The longest root mm	12.1	4.2	0.5	0.3	2.2	1.8	0
Rooting %	76.2	42.9	11.1	7.4	50.0	16	0
Browning %	9.5	1.0	0	0	2.1	0	100
Sprouting %	92.9	90.5	100	36.1	70.8	86.7	0
The longest shoot mm	21.6	11.0	29.2	7.2	17.8	8.1	0

Natural populations of *R. islandica*, *R. indica* and *R. x brachyceras* in/ around rice fallow paddy fields (a and b) observed. At the field (a), the number attached to the triangles and quadrats shows the number of plants. At the field (b), the black bars show the number of small silique form and the white circles show large silique form of *R. islandica*. The black triangles show *R. indica* and the white triangles show *R. x brachyceras*, as illustrated with Figure 12.

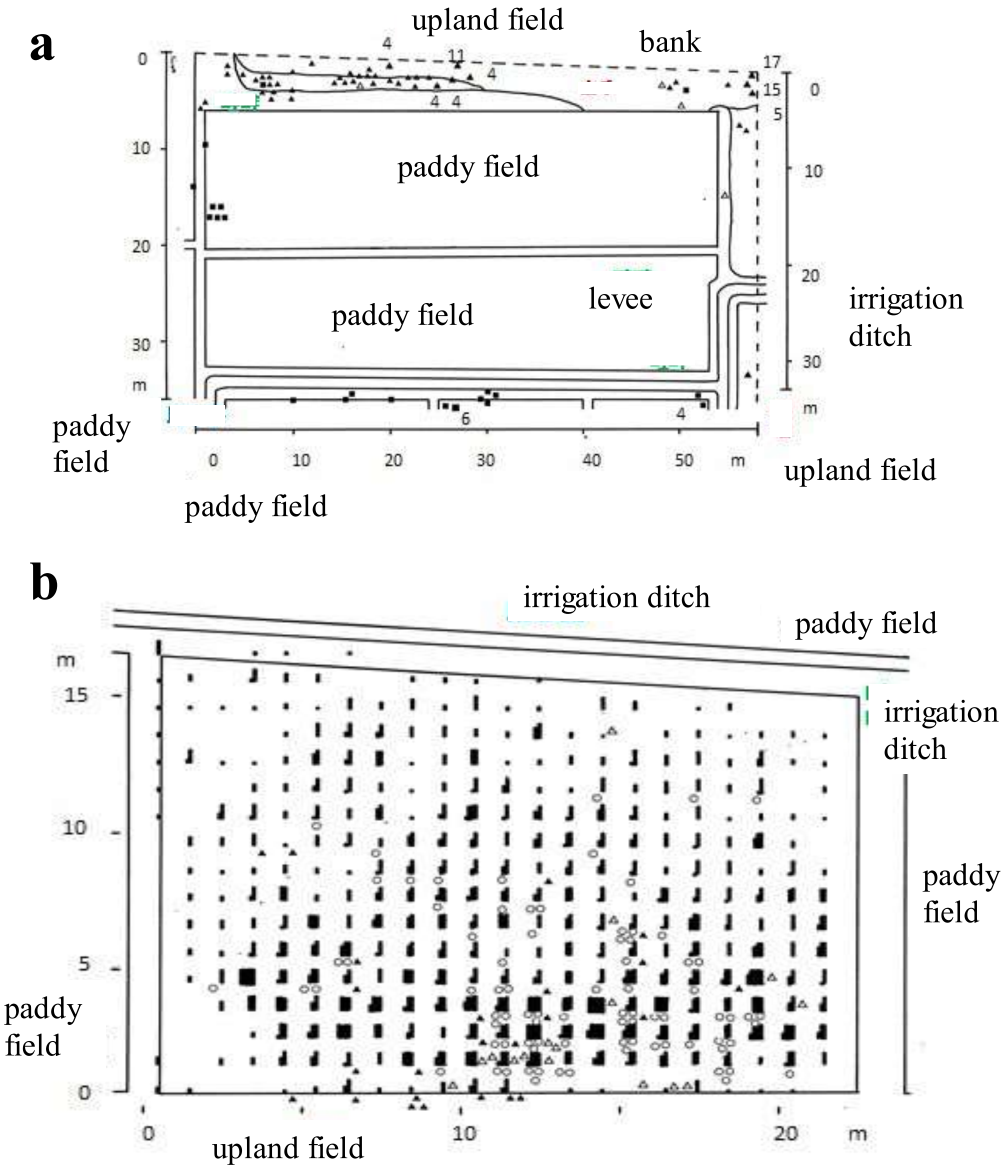


Figure 12. Distribution of *R. islandica*, *R. indica* and their hybrid around rice paddy fields

a, ■ *R. islandica*; ▲ *R. indica*; △ *R. x brachyceras*. b, ▌ *R. islandica/* plants per m^2.

AFLP markers

DNA extraction was performed on young leaf tissue ground in liquid nitrogen and incubated in 1.5-ml tubes containing 0.5 ml of buffer A for 10 min at 60 °C by using CTAB (hexadecyl-trimethyl-ammonium bromide) methods (Murray and Thompson 1980). The AFLP procedure was performed according to Applied Biosystems (2005), Bai et al. (1999), and Suyama (2001) with some modifications. Amplification reactions were performed according to the same protocol. Five primers associated with *Eco*RI (E+AAC, E+AAG, E+AGG, E+ACT, and E+ACA) were used in combination with 5 primers associated with *Mse*I (M+CAG, M+CTG, M+CTA, M+CAT, and M+CAA). Five microliters of amplification products were loaded onto a 5.75% denaturing polyacrylamide gel (LONZA) and electrophoresed in 1× TBE for 1 h. Bands were detected using the silver staining protocol described by Cho et al. (1996). The bands were detected on the gel at the finest level of sensitivity by Lane Analyzer (ATTO), the raw data were adjusted, and then the visible and reproducible bands were scored for accessions as present (1) or absent (0). The dendrogram of the AFLP markers was constructed using the neighbor-joining and UPGMA methods (Nei and Kumar 2000) with the bootstrap analysis (PAUP* ver. 4.0) and the hierarchical cluster analysis (group average method, SPSS ver. 21) on all data matrices of materials used as shown in Figure 13. AFLP dendrogram shows a very clear phylogenetic tree. Therefore, *R. x brachyceras* is the natural hybrid between *R.islandica* and *R. indica*.

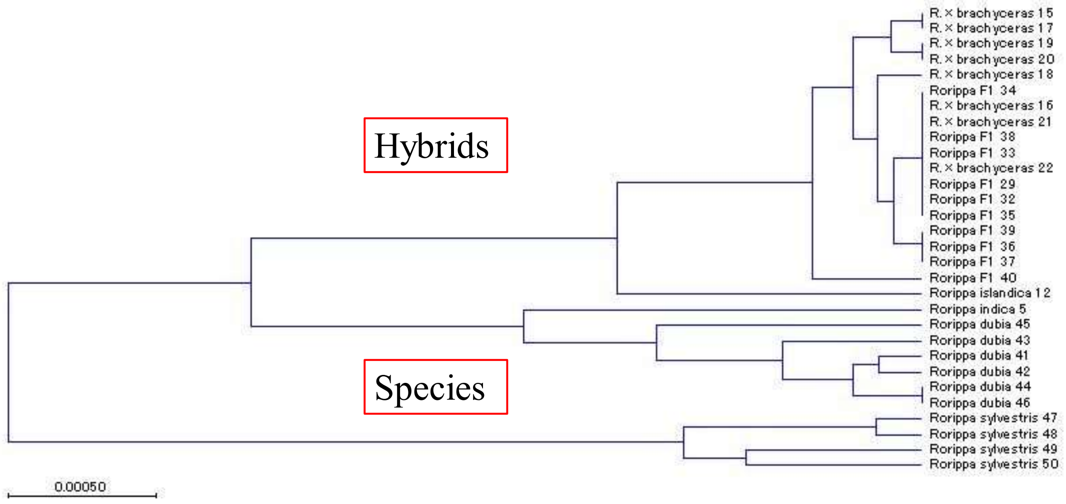


Figure 13. AFLP dendrogram of *Rorippa* by UPGMA

Evolution of the Poaceae

The grass family is not the largest in terms of species and genera, coming after Compositae and so on, but its importance is beyond doubt for it provides the grasslands which occupy a third of land's surface, and the cereal crops upon which much of the world's population depends for its food. The grasses are a successful family, in which three themes constantly recur: their adaptability to changeable environments; their ability to coexist with grazing herbivores an with man; and their possession of a distinctive lifeform. The life cycle of most grasses is strongly seasonal. Perennials become dominant when the season is averse to grow. Annuals overwinter as seed, a strategy generally regarded as more advanced because of the high standard of reproductive efficiency required (Clayton and Renvoize 1986).

Chapman (1996) have written an excellent introduction on Poaceae as follows. Both Poaceae (rice order) and Cyperaceae had differentiated from Commelinales. The Poaceae contains about 10,000 spices. Long before *Homo sapiens* became conspicuous, grasses had and were evolving their distinctive features. Grasses have linear leaves and small green flowers. Thise are generally drought tolerant. The features just outlined combine to fit grasses for open habitats so that they tend to occur as pioneer or early colonists. A perennial grass is well adapted to vegetative reproduction. As with many other angiosperms, grasses demonstrate the evolution of annual or ephemeral forms from perennial forebears, and here the changeover is an interesting one.

Many annuals, wheat and barley among them, retain tillering ability and a tiller with its adventitious roots can be separated from the mother plant and propagated independently. What conditions annualism is a massive commitment to seed production, sufficient to senesce the plant. The situation is irreversible and genes from *Agropyron* introduced into wheat can create a perennial habit. The emergence of C4 photosynthesis seems likely to be due to dearth of CO2 in Tertiary atmospheres. The dawn of agriculture meant not only that preferred plants were recognized but, additionally, others were brought into cultivation. Since weeds survive independently of having to be planted and only fed and watered incidentally, they create an impediment to agriculture.

The Poaceae are anemophilous, which have grown under the various environment. The Poaceae had dispersed widely to the whole earth (Hotta 1974, Tamura 1974).

Growth Habit and Growth Pattern of C*oix lacryma-jobi* var. *ma-yuen* and var. *lacryma-jobi*, Poaceae

In the present study, the differences between the ecogenetical characters on the growth habit and growth pattern of an ecogenetically annual cultivated variety, C*oix lacryma-jobi* var. *ma-yuen* (Sakamoto et al., 1980), and its closely related wild perennial, C*oix lacryma-jobi* var. *ma-yuen* has been recognized as a domesticated annual species by taxonomists (Makino 1948; Ohwi 1953), but both var. *lacryma-jobi* is a wild perennial. The relation between growth habit and growth pattern of those two varieties were compared. C*oix lacryma-jobi* var. *lacryma-jobi*, Gramineae, are compared in order to elucidate some experimental evidences to the problem of intraspecific differentiation from perennial form to ecologically annual one.

Two varieties of C*oix lacryma-jobi* L. var. *ma-yuen* and var. *lacryma-jobi,* two F_1 and one F_2 hybrid strains were used in this study. C. *lacryma-jobi* L. var. *lacryma-jobi* (strain no. 76501) is a wild variety collected in Kamakura-shi, Kanagawa Prefecture in 1975. C. *lacryma-jobi* var. *ma-yuen* (Roman.) Stapf is a domesticated variety (strain no. 76505) obtained from the Agricultural Station of Toyama Prefecture in 1975. These two varieties were crossed reciprocally in 1975 (cross ability ca. 60-70%) and obtained two F_1 hybrid strains, i.e., 76506 (76501 x 76505) and 76508-1 (76505 x 76501). An F_2 progeny (76508-2) was obtained from 76508-1 which was isolated from the other strains in 1976 in order to avoid pollination by alien pollen grains.

Many floristic workers described that C. *lacryma-jobi* L. var. *lacryma-jobi was* a perennial plant but var. *ma-yuen was* an annual one (e.g., Makino 1948; Ohwi 1953). All plants of C. *lacryma-jobi* L. var. *lacryma-jobi* and 22.2-88.9% of var. *ma-yuen* survived in the growth cabinets. Under the upland field plot the survival rate of var. *lacryma-jobi* was 80% in 1976 and 16.7% in 1977. Var. *ma-yuen* did not survive in 1976 and 1977. In F_1 strains none of 76506 survived, but 16.7% of 76508-1 did. The two varieties died under lower temperature (frost, under C and D plots in Table 30) or higher temperature (dryness, under A plot). Murakami and Harada (1958) observed that 20% of var. *ma-yuen* and all of var. *lacryma-jobi* and their F_1 strains survived in next growing season under upland field in Kyoto. The survival rate of F_2 was ca. 80% (Murakami 1961) in Kyoto and 61% in Tokyo in the present study. Moreover, two strains of var. *ma-yuen* collected from North Halmahera, Indonesia in 1976, have been vegetatively maintained in an unheated greenhouse during at least three years (Sakamoto et al., 1980). Judging from these observations, it is concluded that *C. lacryma-jobi* var. *lacryma-jobi* is perennial plant, while var. *ma-yuen* is a potentially perennial but ecologically annual plant having weak cold resistance.

The grain of var. *ma-yuen* germinated more rapidly than that of var. *lacryma-jobi*. The grain germinating pattern of F_1 was intermediate between the two parents as shown in Fig. 18 and the pattern of F_2 showed the same pattern as var. *ma-yuen* parent as shown in Fig. 19. The rapid grain germination of var. *ma-yuen* as well as F_2 indicates one of the characteristics of annual plants.

The plants height of var. *ma-yuen* increased more rapidly than that of var. *lacryma-jobi*. Similarly, the number of tillers of var. *ma-yuen* increased and reached a plateau more rapidly than that of var. *lacryma-jobi*. Therefore, it is thought that the former variety indicates annual growth pattern, while the latter shows perennial one. The growth pattern of F_1 was intermediate between the two parents. The frequency distribution of plant height of F_2 showed a bimodal curve as shown in Fig. 21. One peak corresponds with the mean plant height of var. *ma-yuen* parent and the other showed transgressive segregation as observed by Murakami (1961). The frequency distribution of the number of tillers of F_2 showed a normal curve as shown in Fig. 23. The peak is in accordance approximately with the mean number of tillers of var. *ma-yuen*. Therefore, the large part of F_2 plants shows vigorous growth with small tillering capacity.

The heading date of var. *ma-yuen* was earlier than that of var. *lacryima-jobi* as shown in Table 30 and 31, and Fig. 20. The early maturity of var. *ma-yuen* is one characteristic displayed by annual plants, while the late maturity of var. *lacryma-jobi* is one of perennial characteristics. The heading date of F_1 was intermediate between the two parents. The frequency distribution of heading date of F_2 showed a bimodal curve. The earlier half part of the curve coincides with that of var. *ma-yuen,* while the latter half part of agrees with the late heading of var. *lacryma-jobi*. Murakami (1961) presumed that the frequency distribution of heading date in F_2 was similar to that of trihybrid (segregation ratio 10:54 = early var. *ma-yuen* type: late var. *lacryma-jobi* type). In the present study, however, the segregation ratio (4:5) did not agree with the above ratio. Moreover, the heading date of two parents was later and the difference of heading date between two parents was less remarkable in this study than in Murakami's data. The variation of heading date, therefore, needs to be reexamined.

The pollen fertility is higher and the protogyny is lower in var. *ma-yuen* than in var. *lacryma-jobi* (Tables 32 and 33). Therefore, the grain fertility of var. *ma-yuen* is higher than that of var. *lacryma-jobi* (Table 32). Moreover, var. *ma-yuen* sets more grains than var. *lacryma-jobi*, but grains were lighter than that of var. *lacryma-jobi* (Table 34). Murakami et al. (1960) reported weak sexual isolation between those two varieties. The same can be said from the pollen and grain fertility of F_1 shown in this experiment also.

The proportional distribution of dry matter into the inflorescences and grains attained ca. 11% (9.1g) of the total plant dry weight in var. *lacryma-jobi* and 20% in var. *ma-yuen* in the end of growing period (Fig. 25). Kawano and Hayashi (1977) reported that the reproductive allocation into grains attained 41.0% (the highest rate) in var. *ma-yuen*. The distribution into the subterranean stems attained 6% (5.0g) in var. *lacryma-jobi* and 2% (0.9g) I var. *ma-yuen* at the end of growing period. Var. *lacryma-jobi* allocates half as much energy for sexual reproduction and three times as much into vegetative one as var. *ma-yuen* does. Also, these characteristics on the reproductive systems suggest that var. *ma-yuen* is an annual form and var. *lacryma-jobi* a perennial one (cf. Kawano 1975).

McNaughton (1975) described that populations of *Typha* in short growing season produced many small rhizomes, since such populations were subject to high rhizome mortality in winter time. *C. lacryma-jobi* var. *lacryma-jobi* produced more tillers with dormant buds and more ratoons from cutting stump than var. *ma-yuen* as shown in Tables 35 and 36. However, there are no correlation between total number of tillers and the number of sprouting tillers wintered or the survival rate. There is a significant but low positive correlation between the number of non-productive tillers and the number of sprouting tillers wintered. Accordingly, there is not very close relation between the tillering capacity and the wintering habit in *Coix*. In order to shed more light on this problem, further physiological and genetical investigations on wintering habit are needed.

Oka and Morishima (1967) observed that the culm segment in perennial strains of *Oryza* rooted more easily than in annual one. It is thought that the rooting from culm is related to the degree of vegetative reproduction. In two varieties of *C. lacryma-jobi* the rooting and sprouting rates from culm segments were rather high, and not significantly different between them. This observation suggests that var. *ma-yuen* is a potentially perennial plant.

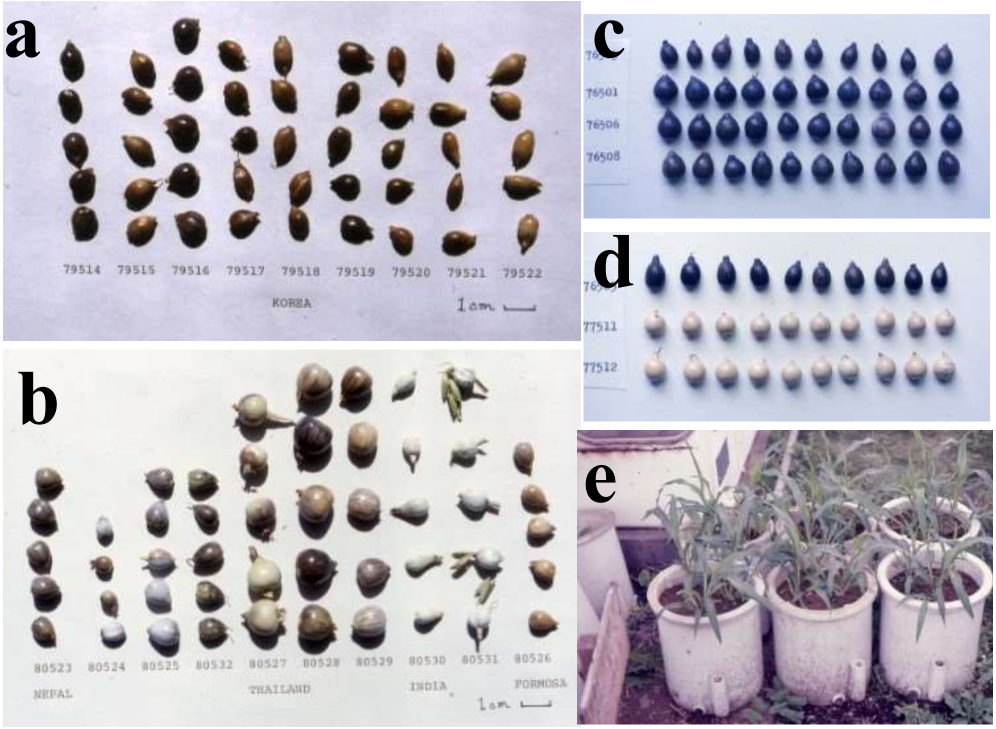


Figure 14. Morphological variation of bract sheath in *Coix lacryma-jobi*
a,b,c,d, bract sheath; e, var. *ma-yuen* (upper) and var. *lacryma-jobi* (below)

Judging from the present results obtained from the comparative studies on growth pattern, reproductive systems and tillering capacity of these two varieties, it is concluded that *C. lacryma-jobi* var. *ma-yuen* is an ecologically annual but potentially perennial plant and var. *lacryma-jobi* is apparently a perennial one as summarized in Table 10.

Table 10. Characteristics of *Coix lacryma-jobi* var. *lacryma-jobi* and *C. lacryma-jobi* var. *ma-yuen*

Characteristics	**var. *lacryma-jobi***	**var. *ma-yuen***
Breeding system	high degree of protogyny	protogyny
Grains per plant	ca. 80	ca. 270
Asexual reproduction by rhizome	present	absent
Germination	gradual, late	simultaneous, earlier
Heading date	late	early
Growth habit	perennial	ecologocal annual
Habitat	creek, roadside, river side	upland field

Growth habit of genus *Zea*

Zea mays (maize, annual), teosinte (Figure 15) and *Tripsacum* are the three New World members of the tribe Maydeae. Teosinte (2n=20), a weedy annual, is a close relative of maize (2n=20). Maze and teosinte differ most in the structure of their female inflorescences and in their chromosome knob patterns. Morphologically teosinte plants often resemble maize. The teosinte spike is very loosely enclosed by a few husks, the rachis of the spike becoming very fragile upon maturity, and the fruit case disseminating easily as shown Figure 15. Maize, with neither natural seed dispersal nor seed dormancy, is wholly dependent upon man for its propagation (Goodman 1995).

The oriental Maydeae (*Coix* and so on) are usually acknowledged to be but distantly related to maize (Mangelsdorf 1974), although there has been occasional speculation that *Coix*, which has knobbed chromosomes in multiples of x=5, is more closely related to maize than the other oriental genera.

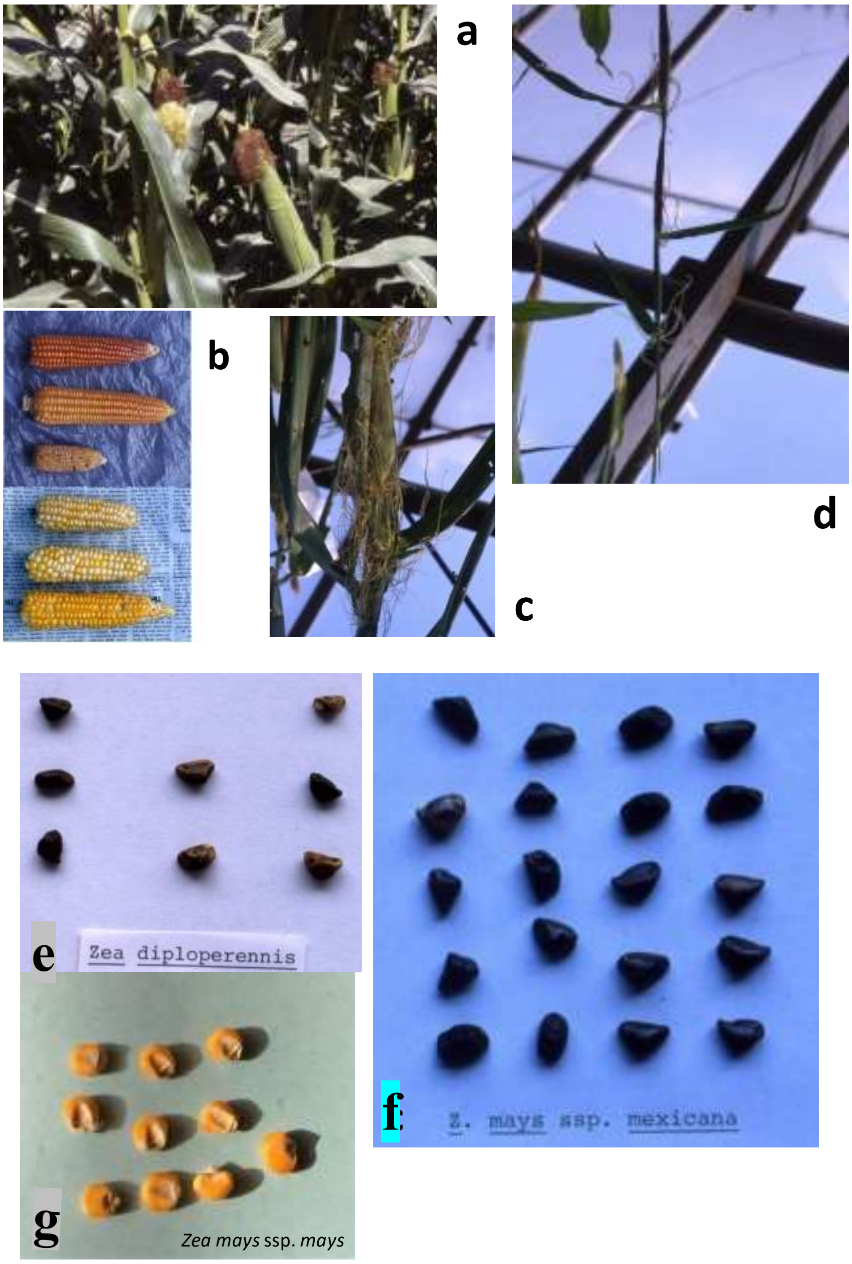


Figure 15. Ears and seeds of genus *Zea*

a, ears of *Zea mays* from Uzbekistan; b, ears of *Z. mays* from Nepal; c, ear of *Z. mays* ssp. *mexicana*; d, ear of *Z. diploperennis* ; e, seeds of *Z. diploperennis*; f, seeds of *Z. mays* ssp. *mexicana*; g, seeds of *Z. mays* ssp. *mays* from Yamanashi, Japan.

Guzman came on a large stand of grass and sent seeds to Iltis (1983, 1987; Fussell 1992). Iltis found that the grown plants had the same number of chromosomes as maize, and that Guzman had discovered a new species, which Iltis labeled *Zea diploperennis*, or perennial teosinte. Iltis had sent me the seeds (Figure 15d, e).

I had participated in the US-Japan Science Seminar, New York Botanical Garden in 1983. At this time, I had directly heard the story of maize evolution from Iltis, and then he had sent me the seeds of *Zea diploperennis*.

Differentiation of ecotype on genus *Agropyron*, Poaceae

The early ecotype (annual) of *Agropyron tsukushiense* (Honda) Ohwi var. *transiens* (Hack.) Ohwi adapted to fallow paddy fields are ecologically and genetically differentiated from the common type commonly found on roadsides, levees and other disturbed habitats (Sakamoto 1961). The closely related *A. humidorum* Ohwi et Sakamoto grows in fallow rice paddy fields, often sympatrically found with the early ecotype of *A. tsukushiense* var. *transiens* (Ohwi and Sakamoto 1964; Sakamoto 1978). Therefore, the relation between growth habit and habitat of those two species was studied.

Field observation:

Four winter fallow paddy fields, designated P-1, P-2, P-3 and P-4, were selected in the suburbs of Mishima-shi, Shizuoka Prefecture. In P-1 a mixed swarm of the early ecotype of *A. tsukushiense* var. *transiens* and *A. humidorum* were found. In P-2 the former was abundant but the latter species rare, while in P-3 the reverse situation was observed. In P-4 the latter species was abundantly grown but the former was very seldom found. The number of seedlings formed by seed and propagules produced from culm segment were counted by 1m^2 quadrat method in a fallow paddy field (P-1) on November 21st, 1975 and November 22nd, 1976. At the same time, 10cm soil surface of the paddy field was dug in order to measure the depth of soil from where seedlings and sprouting propagules are found.

The number of germinating seeds and the number of sprouting or non-sprouting segments found in soil clods (50 cm length x 50 cm width x 10 cm depth = 0.025 m^3) in two fallow paddy fields (P-2 and P-3) were counted on January 16th, 1978. Such soil clods were sampled randomly at 3-5 sites in a paddy field. The relationship between the number of nodes of culm segments and their sprouting rate of *A. humidorum* was examined using same methods in a paddy field (P-4).

Seed germination and sprouting of culm segment under several conditions:

Three used strains were collected and observed in Mishima-shi, Shizuoka Prefecture. The seeds used were stored under three different water conditions, i.e., upland, lowland and dry conditions, and they were kept under five different temperature conditions, i.e., 1) daytime 35 C, nighttime 25 C; 2) daytime 25C, nighttime 15C; 3) 20 C constant, 4) 6 C constant; and 5) natural temperature conditions in 1976. The experiment consists of 14 water and temperature condition plots. Under the upland condition, seeds were packed into nylon-net bag and then stored in the loam soil which was watered at intervals of several days. Under the lowland condition, they were stored in the submerged loam soil. Under the dry condition, they were stored in the sealed can containing silica gel. At the interval of 15 days stored seeds were taken out from those experimental plots and used for the germination tests. The germination tests were conducted with the unglazed germination plates under the conditions light unglazed germination plates under the conditions light 8,000 lux and 25 C constant.

The culm segments having one node were stored under the upland and lowland conditions and they were kept under four different temperature conditions, i.e., 1) daytime 35 C, nighttime 25 C; 2) daytime 25 C, nighttime 15 C; 3) 20 C constant; 4) natural temperature conditions, in 1975 and 1976.

Therefore, the experiment consists of eight water and temperature condition plots. At the interval of 15 days 30 stored culm segments were taken out from each plot and used for the sprouting test. The sprouting test was carried out on the wet filter paper in Petri dish under continuous light 8,000 lux and 25 C constant.

According to Sakamoto (1978), the natural life cycle of the early ecotype of *A. tsukushiense* and *A. humidrum* shows characteristics of a typical weed in winter fallow paddy fields. At around the maturation stage of those two species, the preparation of rice cultivation is started. During this practice seeds and culms or stumps of those species are dispersed uniformly in the soil of the paddy field. During rice cultivation in summer, they were preserved in dormant state. In the middle of September seeds and propagules start to germinate or sprout and young plants are in tillering stage when rice plants are harvested in October- November. Therefore, these two species are temporally segregated their habitat from rice plants. They grow often sympatrically and they have adapted very successfully to winter fallow paddy fields. However, in the present study a remarkable difference as to the mode of reproduction was recognized between these two species. As shown in Table 38, 39 and 40, in natural habitats the clone of early ecotype usually dies within a year and reproduces only sexually by seeds. So, it is just like an annual plant in spite of perennial under upland condition. Therefore, this ecotype is defined as an ecologically annual but potentially perennial species. On the other hand, *A. humidorum* reproduces both sexually by seeds and asexually by propagules produced from culms.

Compared with the common type, the early ecotype and *A. humidorum* show clearly the adaptability to paddy fields. For example, seeds of those species are maintaining the germinating ability in D plot (natural temperature under lowland condition). According to Ohwi and Sakamoto (1964), adaptation to moist environment is one of the most pronounced characteristics of *A. humidorum*. There have been observed two distinct characters of this species which imply high adaptiveness to the habitat of winter fallow paddy field. One is the formation of an abscission layer at maturity on the node below the flag leaf. Thus, from this node on upward the spike is easily removed from the rest of plant by wind or other physical forces. The other is the perennialization of culm with the exception of the upper most internode and spike. New shoots and roots are produced very easily from the nodes when the condition is favorable.

As was shown clearly in this experiment (figs. 27 and 28) dormancy of seeds and culm segments from June to September under lowland condition is also additional adaptive character of this species. Judging from those observations, it is concluded that *A. humidorum* has more positive adaptation to propagate vegetatively by perennialized culms or clones than to reproduce sexually by seeds.

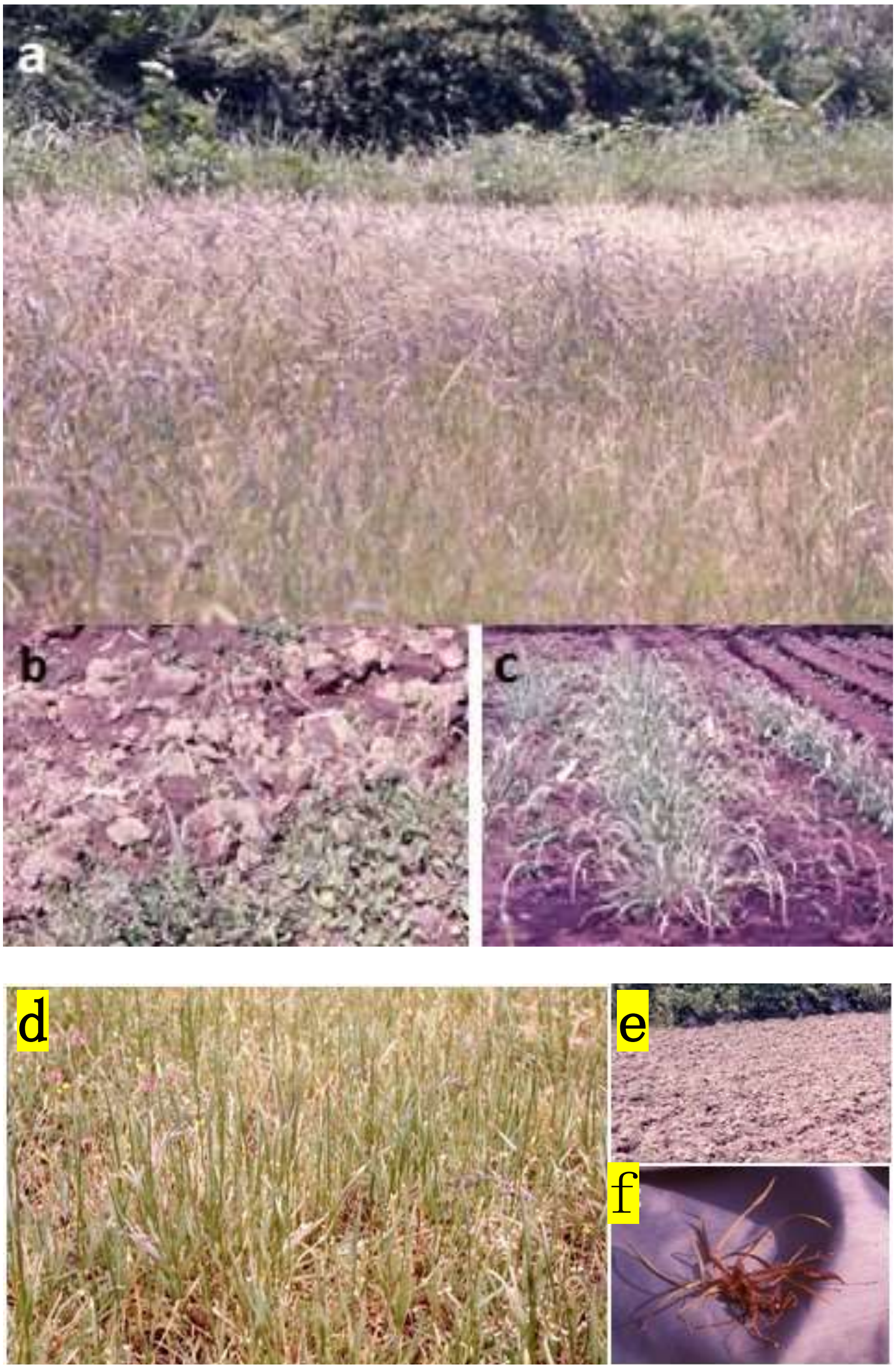


Figure 16. Weeds of genus *Agropyron*

a, early ecotype of *A. tsukushiense* in a fallow paddy field in Mishima, Shizuoka prefecture; b, early ecotype on levee after spring plowing; c, common type of *A. tsukushiense* at the field in Tokyo Gakugei University; d, a sympatric population of early ecotype and *A. humidorum*; e, after spring plowing in the same sympatric population; f, sprouting from culm section in soil of fallow field after spring plowing.

It will be quite interesting that two closely related species adapted to the same environmental conditions display quite contrasted adaptive strategies to maintain their natural populations in winter fallow paddy fields.

Life history of genus *Secale*, tribe Triticeae

Rye has the strongest cold tolerance among the cereals grown in Temperate zoon. Farmers can sow both in winter and spring, but the yield is fewer in spring than in winter. An annual weedy group of *Secale* had differentiated from the perennial outcrossing group of *Secale montanum* in the Far East (Figure 17). This annual weed had lost the shattering habit, become erectness and larger grains under the domestication process, and then had domesticated to *Secale cereale* (outcrossing annual). On the other hand, the group of *Secale montanum* had differentiated into *S. silvestre* and *S. vavilovii* (self-pollinated annual). Under this process, the adaptation had occurred in the rearrangement of tree chromosomes and the change from perennial to annual.

Based on archaeological evidence, the domestication had been begun since ca. 3,000~4,000 BC. On the early 20 AD, a third of European people had eaten rye bread, while they had gradually changed to eat wheat bread (Stebbins 1950, 1957, 1958; Riley 1955, Khush and Stebbins 1961, Khush 1963, Suneson et al. 1969, Evans 1996).

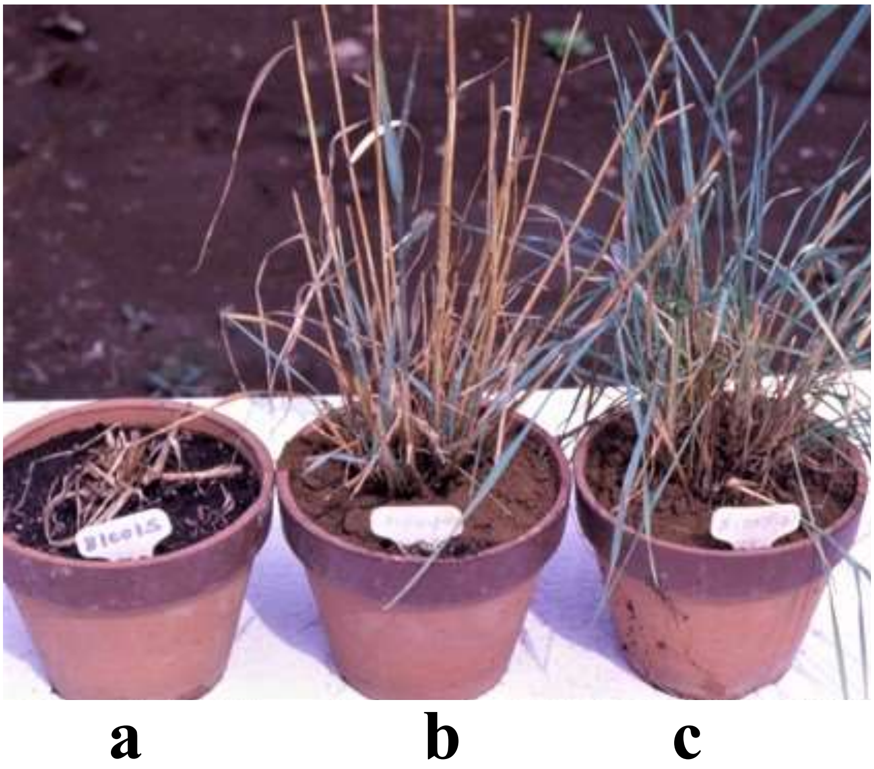
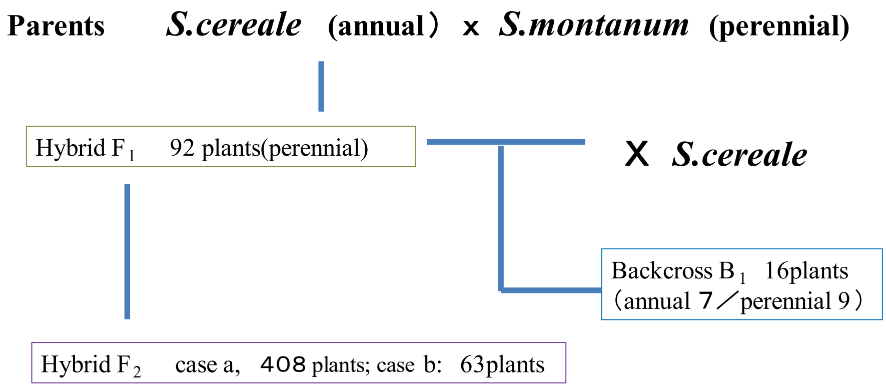


Figure 17. Hybrid F$_1$ (c; perennial) between *Secale cereale* (a; annual) and *S. montanum* (b; perennial)

The wild of *S. cereale* distributes from Central Europe, to Balkan peninsula, Anatolia, Israel, Trans-Caucasia, Iran, Central Asia; Afghanistan, and additionally disperses a small population isolated in South Africa. All species are diploid (2n=14). These species invade into the disturbed habitats by natural and artificial situation, especially wheat/barley fields such as weed. *Secale cereale* was the secondary crop which had been domesticated from the companion weedy rye. When wheat/barley had been dispersed to the north or highland region, these crops had been cultivated under the cold and barren land. Occasionally, when the sever cold weather attacked to fields, the yield of wheat/barley decreased, but rye did not so much decrease. Therefore, *S. cereale* had become from a weed to a domesticated plant, because weedy rye had the strong tolerance against for cold (Vavilov 1926). The domestication process still continued to progress on fields (Sakamoto and Kawahara 1979).

This domestication process is very interesting when we compare with the process of Indian millets. Since the limiting factor is cold tolerance on the case of rye, while that is drought tolerance on the Indian millets. Namely, rye was domesticated from companion weed with wheat/barley, while Indian millets were domesticated from companion mimic weeds with rice. The main factor was drought tolerance for growing in the Decan Plateau (Kimata 2016).

As shown in Figure 18, the hybrid F1 between *S. cereale* (annual) and *S. montanum* (perennial) was perennial. The perennial growth habit was dominant, but the segregation rate of F2 is very complex, some plants were no heading and necrosis. The growth habits were not decided through a major gene. These materials were provided from Kyoto University.



Segregation of growth habit :
Case a: annual 80／perennial 201／no heading 28／dead 99
Case b: annual 6／perennial 39／no heading 7／dead 11

Figure 18. Artificial Hybridization of *Secale*

Annual is clearly dominant to perennial. There are so many characteristics related to the growth habit, that is, morphology, ecology and genetics. The number of nonproductive tillers was closely related to maintain dormant buds for polycarpic. However, *S. cereale,* annual has not maintain nonproductive tillers (late-emerging heads and foliage buds) by the end of July. The nonproductive tillers of *S. montanum* are 21~30, that of Hybrid F1 are 51~60 such as tussock. The annual of Hybrid F2, have not nonproductive tiller, but the perennial have so variable number of tillers, 1~90. Under the domestication process, the artificial selection performs for decreasing in the number of nonproductive tillers.

Domestication process of wheat

There are many important cereals and fodder crops belonging to sub-family, Festucoideae (family, Poaceae). In tribe Triticeae (Table 11), genus *Agropyron* consisted of only perennials, *Secale* and *Hordeum* contained both annual and perennial, moreover *Triticum* and *Aegilops* consisted of only annuals (Satake 1964, Sakamoto 1991, 1996; Kihara ed. 1954; Clayton and Renvoize 1986).

Fifteen genera of tribe Triticeae, Gramineae, are classified into two major groups from their geographical distribution, the Mediterranean group and the Arctic-temperature group (Sakamoto 1973). The former consists of mostly self-fertilized annual species, while the latter largely perennial (both self- and cross-fertilized). The rapid adaptive differentiation of the Mediterranean group occurred during the formation of the Mediterranean climate most probably in the Quaternary. The climate is characterized by hot, dry summers and cool, moist winters. Those annual species have adapted to the conditions in winter. Therefore, most winter annuals seem to have originated in Mediterranean-Central Asiatic regions.

Compering the distribution and growth habit among 15 genera of Triticeaae, the most annual species had distributed from Mediterranean to Central Asia, while the most perennial species had distributed in circumarctic and temperate zones.

The region from Mediterranean to Central Asia have been dry land in summer under Mediterranean climate. Here had been the place where people had domesticated wheat, barley and so on, and they had created an ancient farming culture about 1,2000 BP. Those winter annuals germinate in autumn, overwinter, bloom, and then bear fruits (Sakamoto 1973). The Triticeae had differentiated quickly many genera and species through the adaptive radiation during the period when the topography had fluctuated rapidly by Alpin orogeny. Therefore, Triticeae indicates morphological diversity, close genetic relative. These species had hybridized among species and genera, then differentiated into allopolyploid or autopolyploid.

Table 11. Classification of 15 genera in the Triticeae（Sakamoto 1974）

Growth habit / Distribution	perennial	perennial+annual	annual	Rachis node with:
Mediterranean-Central Asistic regions	*Festucopsis* (2x)	*Haynaldia* (2x, 4x)	*Aegilops* (2x, 4x, 6x)	sollitary spikelets
		Secale (2x)	*Eremopyrum* (2x, 4x)	
			Henrardia (2x)	
			Heleranthelium (2x)	
			Triticum (2x, 4x, 6x)	
			Crithopsis (2x)	spikelets in group
			Taeniatherum (2x)	
Arctic-temperate regions of te world	*Agropyron* (2x, 4x, 6x, 8x, 10x)			solitary spikelets
	Asperella (4x)	*Hordeum* (2x, 4x)		spiklets in group
	Elymus (4x, 6x, 8x)			
	Psathyrostachys (2x)			
	Sitanion * (4x)			

* A North America genus　　Green character: genera used in this book

Modified Sakamoto (1973)

An annual is a plant that completes its life cycle and dies within 12 months, though the life span may overlap two calendar years because of wintering. There are two categories of annual life cycle, that which is ended more or less abruptly with flowering and seed set and that which has a potentially indefinite length of life that is usually ended within a year by a climatic event (Harper 1977). The former category is “true” annual in the strict sense, while the latter ecological annual and potential perennial. In the first category are many of the above grasses of Mediterranean climates and arable land. On this arable land, their life for an annual in a crop is relatively safe until harvest and they can use the period in continuous cycle of growth. However, the adaptive value of the second category has been hardly studied yet.

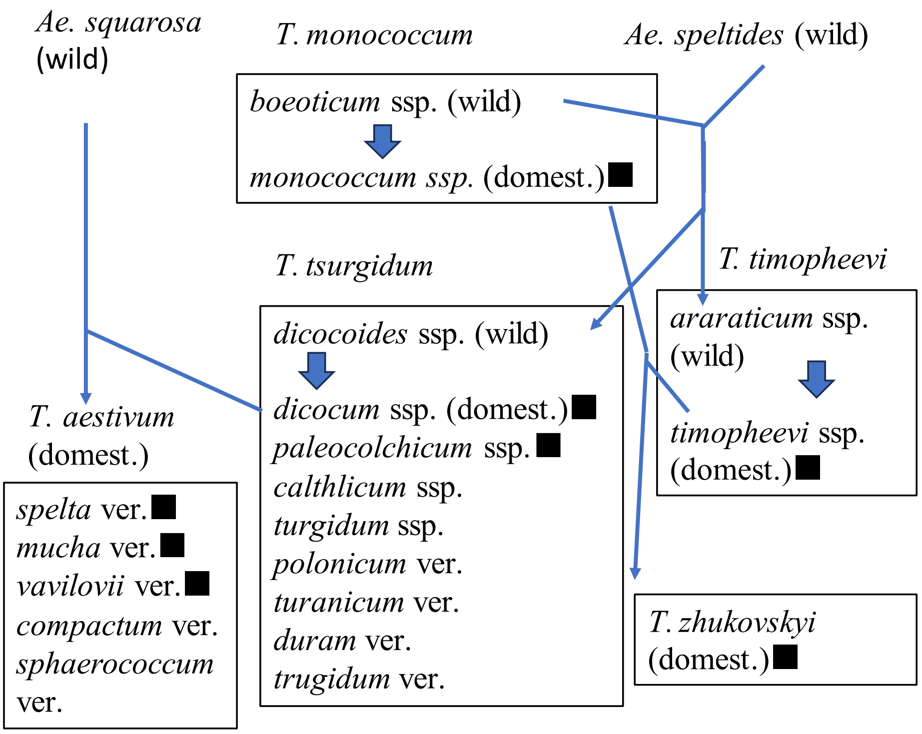


Figure 19. Origins and domestication of five groups in genus *Triticum*

→ Hybridization and doubling; ⬇ Domestication; ■ hulled grain.

(modified Sakamoto 1985,1996; Ohta original)

As shown in Figure 19, the domestication process had been progressed with such as annual. It had been very complicate, because many species were involved with the process. Sakamoto (1996) have categorized five groups of wheat as shown in Table 12. There are both wild subspecies and domesticated subspecies on *T. monococcum*, *T. turgidum* and *T. timopheevi*. Namely, those wheats had been domesticated from their wild subspecies, that is to say, from each *T. monococcum* ssp. *boeoticum*, *T. turgidum* ssp. *dicoccoides* and *T. timopheevi* ssp. *araraticum*. However, it was no wild species on *T. aestivum*.

Based on numerous papers, *T. aestivum* was domesticated as a hybrid between *T. turgidum* and *Ae. squarrosa*. *T. aestivum* was amphidiploid and a secondary crop which had involved with a companion weed. *Ae. squarrosa* had distributed from Trans-Caucasus, Eastern Turkey, Iran, Afghanistan, Central Asia to Western China. In Iran, *Ae. squarrosa* is a weed in wheat fields. T. aestivum had accepted D genome from the subspecies grown in East cost of Caspian Sea and Trans-Caucasus, and then it had been domesticated in this region.

Ehrendorfer (1965), Ornduff (1969) and Stebbins (1974) have pointed out the relationship between self-fertilized annual and heigher polyploidy, and then have avoided the disadvantage of homozygous genotype (Table 3 and Table 11). These species are cross-fertilized by wind pollination, and same species are self-fertilized with high self-pollination rate. However, tribe Triticeae indicates that many polyploid spices do not relate to their growth habit.

We have gone on an expedition to Central Asia in 1993, and collected many species of Triticeae as shown in Table 12 and Figure 20. The number of accessions were *Triticum* (47), *Hordeum* (37), *Aegilops* (26), and *Agropyron* (17). Even now, their natural hybridization has continued among them on wheat fields. Those scientific names were identified in detail by Plant Germ-Plasm Institute, Kyoto University. We conducted their field experiment in 1994. For the comparison with those *Hordeum* species, *H. bulbosum* (2n=14, 28) was grown. *H. bulbosum* was a perennial with ryzom and polycarpy.

Table 12. Tribe Triticeae collected in Central Asia

Locality	Species	germination %	germination date
Kazakhstan	*Aegilops cylindrica* var. *typica*	100	May 22
Kazakhstan	*Ae. triuncialis* ssp. *eu-triuncialis* var. *typica*	100	May 24
Kazakhstan	*Ae. squarrosa* ssp. *eu-eusquarrosa* ver. *typica*	100	May 14
Kazakhstan	*Ae. crass* var. *typica* or var. *macrathera*	100	May 26
Kazakhstan	*Ae. crass* var. *macrathera*	100	May 22
Kazakhstan	*Ae. cylindrica* var. *pauciaristata*	60	May 27
Kazakhstan	natural hybrid; *Triticum aestivum* x *Ae* . sp. grew with *Ae. cylindrica* var. *typica* or *Ae. triuncialis*	0	
Kazakhstan	natural hybrid; *Triticum aestivum* x *Ae.* sp. grew with *Ae. cylindrica* var. *typica*	0	
Kazakhstan	*Ae. cylindrica* var. typica (sympatric)	100	May 18
Kazakhstan	*Hordeum spontaneum*	70	May 19
Kazakhstan	*H. vulgare* (6 rowed)	100	May 29
Kazakhstan	*H. vulgare* (2 rowed)	100	May 6
Uzubekistan	*H. vulgare* (6 rowed)	80	May 30
Uzubekistan	*H. vulgare* (2 rowed)	80	May 16
Uzubekistan	*H. spontaneum*	80	May 18
Kazakhstan	*T. aestivum*	90	May 14
Uzubekistan	*T. aestivum*	100	May 14
Uzubekistan	*Secale cereale*	100	May 24
Uzubekistan	*Triticale*	90	May 6

Figure 21 is shown an ancient field of wheat which is contaminated with many weedy species, for example, poppy, corn cockle, rye, oat and so on. Barley, *Hordeum vulgare* is a self-pollinating diploid with 2n=2x=14. Tetraploids have appeared spontaneously but are a negligible part of crop. The wild and weed races are usually designated *H. spontaneum* but, biologically, they belong to the same species as the domesticated races (Harlan 1995).

Figure 20. Natural hybridization of wheat in natural population, south Kazakhstan.

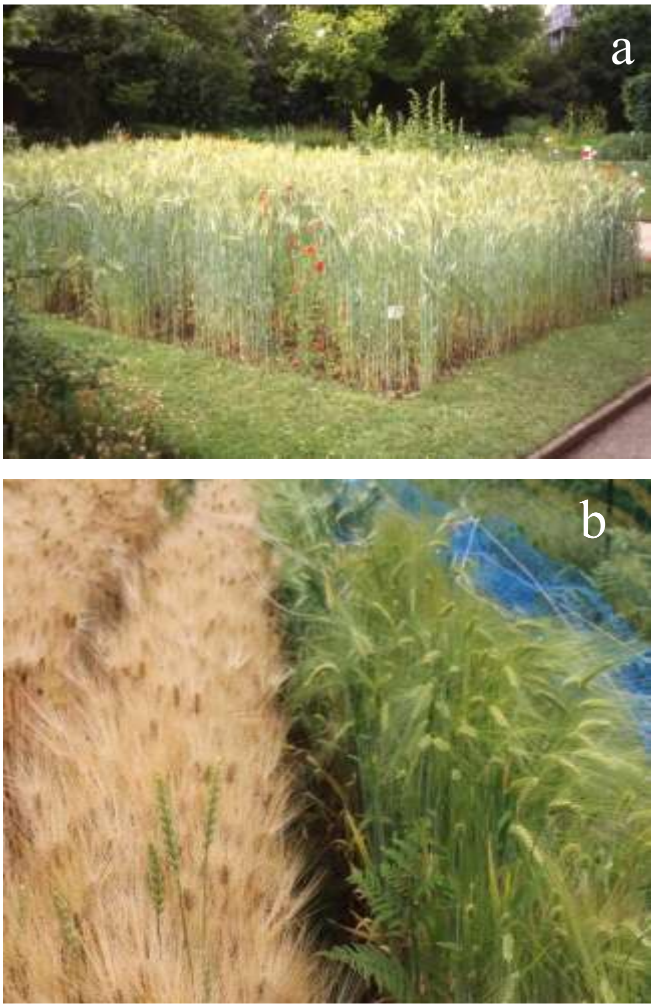


Figure 21. Wheat and Barley

a, an ancient wheat field (restoration) at the botanical garden of Free University Berlin, Germany; b, a barley field at Kosuge, Yamanashi, Japan.

Growth habit of *Sorghum*

Sorghum is highly diversified genus (de Wet 1978, Heran 1979, Sakamoto 1988). *Sorghum bicolor* (L) Moench is an annual plant (2n = 20, diploid, Figure 22) derived from *S. bicolor* var. *verticilliflorum* in Eastern Africa.

S. halepense (L) Pers. is a perennial weed (2n=40, tetraploid) and classified two subspecies. The Mediterranean ecotype is small plant with slender leaves, and distributes from Asian Minor to Western mountainous region in Pakistan. The tropical ecotype is a bigger plant with wide leaves (2n=20), and distributes from South India to the Islands of Southeast Asia.

S. propinquum (Kunth) Hitchcock is a perennial diploid (2n=20), and distributes from Sri Lanka to South India, Myanmar and the Islands of Southeast Asia. In Philippines, the hybrid between this spices and *S. bicolor* is a perennial and serious harm weed. The hybrids among *S. bicolor*, *S. halepense* and *S. propinquum* are perennial triploid/tetraploid which propagate vigorously by the ryzomes. Also, this sign means that a perennial growth habit is dominant trait. The purpose is breeding for the prevention of soil degradation and for fodder crop (Quinby *et al.* 1958, Cox *et al*. 2018).

In Central Asia, we collected 52 accessions, and classified into five types according to panicle form. The broom type (15 accessions) was a broom sorghum. This type was grown in kitchen gardens everywhere in West Turkestan and was an excellent material for making brooms because of the long sparse panicle (about 70 cm). The brooms were also sold in many bazaars. The weedy type (3) had a sparse panicle with many tillers. The sugar A type (7) had conical panicles and a large variation. The sugar B type (14) had a spear like panicle. The number of tillers was a few. These sugar types were maintained for genetic resources of sugar production at Leningrad University. The grain type (10) had a drooping ovate-compact panicle and few tillers. In this region, *S. bicolor* was remarkably various, but no perennial weeds.

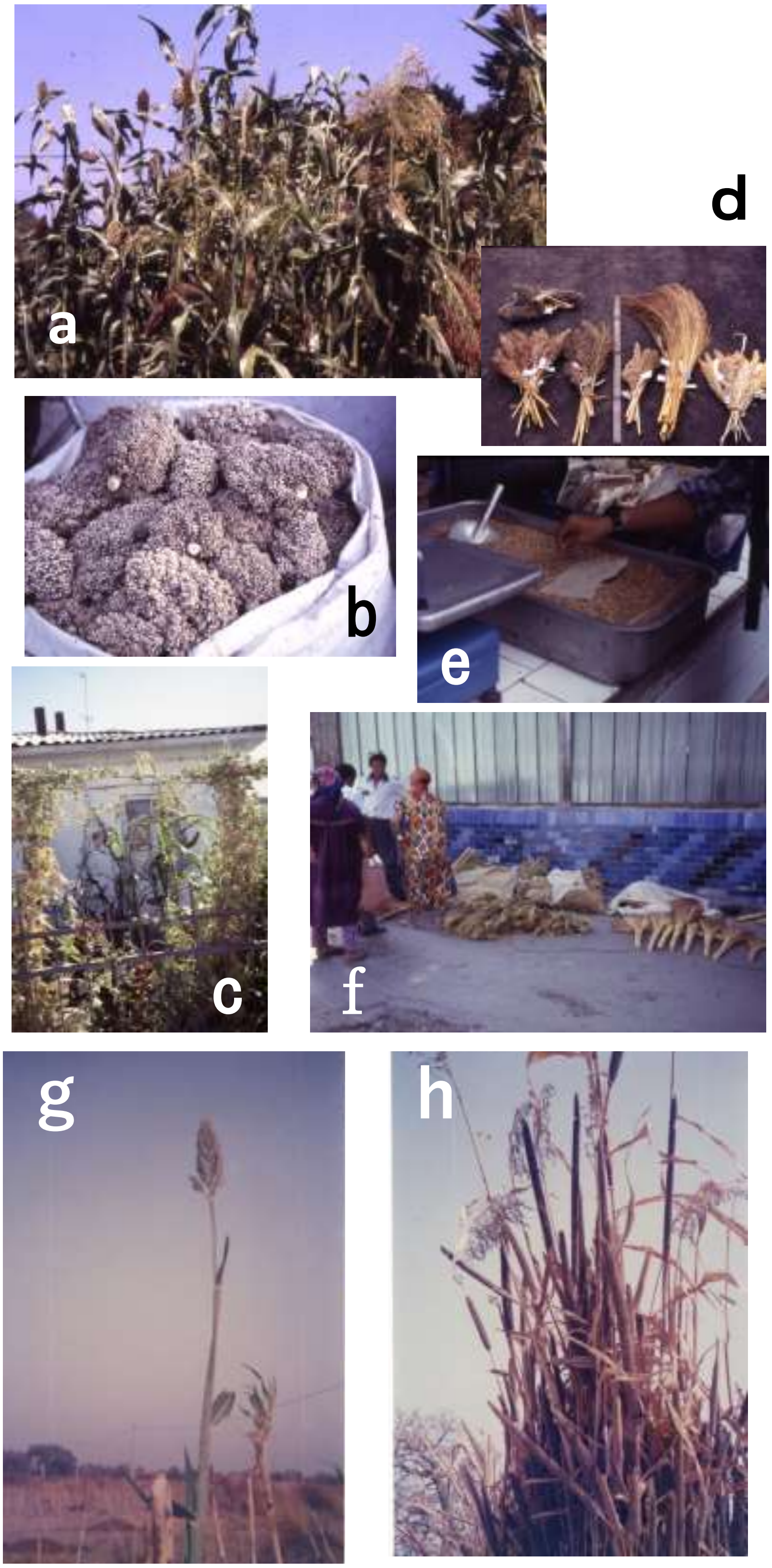


Figure 22. ***Sorghum bicolor*** **in Central Asia and Africa**

a, from India ; b, c, d, e, f; Bazar in Central Asia ; g and h, from Cote d'lvoire, Africa (Konishi photo).

Polyploidy and growth habit of genus *Oryza*

Genus Oryza, Poaceae consists of about 20 wild spices and two domesticated species as shown in Table 13. There are annual diploid (3 species), annual/perennial (5), perennial (7), and perennial tetraploid (8) (Oka and Coworkers 1980, Morishima 2001).

Domesticated rice, *O. sativa* is annual/perennial diploid. The ancestor, *O. rufipogon* is also annual/perennial growing in Tropical and Subtropical regions of Asia. Both species are complicated their speciation, because of their diversity. Ancestral species of *O. sativa* had been domesticated from a wild perennial *O. rufipogon*. *O. sativa* had been selected artificially and was become an ecological annual which increased seed production by self-fertility. At the same time, if it was warm winter, the plants grew by many ratoons after harvest and flowered again. It meant that *O. sativa* was perennial as for botanically. The natural selection has functioned on the habitats, at the same time, the artificial selection have been yearly worked by farmers under the cultivation cycle. Moreover, the upland rice had been secondary adapted to dry condition and then progressed to ecological annual growth habit under the drought or cold condition. The cultivation cycle was better within a year for farmers and plants.

O. glaberima Steud. is an annual diploid which had domesticated in West Africa. The ancestral species have been *O. barthii*, an annual diploid. Another African wild rice, *O. longistaminata* is a perennial diploid with self-incompatibility, but propagated both by seeds and subterranean stems.

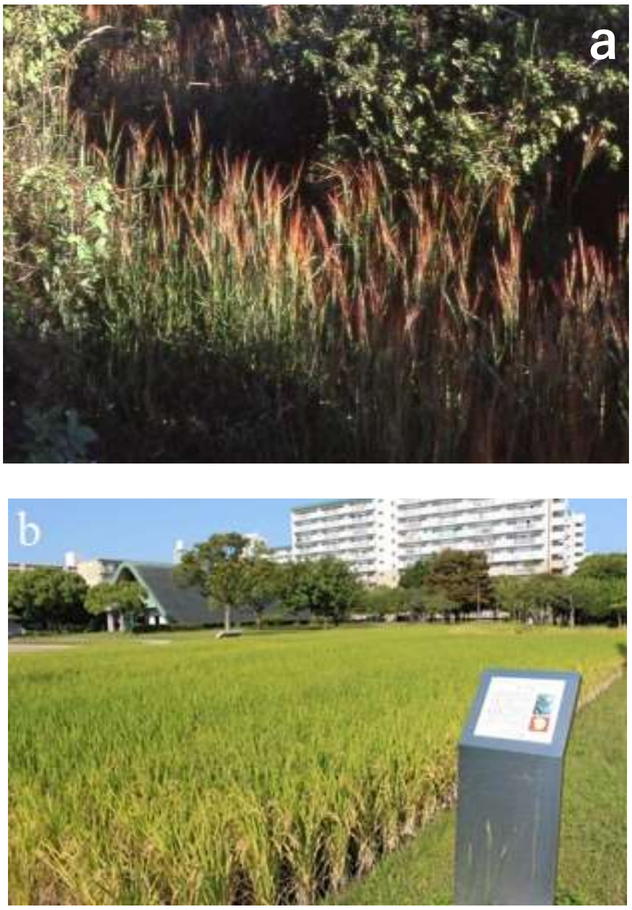


Figure 21. Rice paddy field

a, wild rice, *O. rufipogon* in Orissa, India; b, ancient rice paddy field (restoration) at archaeological site Itatsuke in

Kyushu, Japan.

Table 13. Some characteristics of genus *Oryza*

Genus *Oryza*	**Chromosome number (2n)**	**Growth habit**	**Genome**	**Distribution**
Section *Oryza*				
***O. sativa* ***	24	A/P	AA	around the world
***O. rufipogon* sensu lato**	24	A-P	AA	Asia, Oceania
***O. glaberrima* ***	24	A	AA	West Africa
O. barthii	24	A	AA	Africa
O. longistaminata	24	P	AA	Africa
O. meridionalis	24	A	AA	Australia
O. glumaepatula	24	A-P	AA	America
O. officinalis	24	P	CC	Asia
O. minuta	48	P	BBCC	Philippines
O. rhizomatis	24	P	CC	Sri Lanka
O. eihingeri	24	P	CC	Africa, Sri Lanka
O. punctata	24, 48	P	BB, BBCC	Africa
O. latifolia	48	P	CCDD	America
O. alta	48	P	CCDD	America
O. grandiglumis	48	P	CCDD	America
O. australiensis	24	A/P	EE	Australia
Section *Ridleyanae*				
O. brachyantha	24	A/P	FF	Africa
O. schlechteri	48	P	-	New Guinea
O. ridleyi	48	P	HHJJ	Asia
O. longiglumis	48	P	HHJJ	New Guinea
Section *Granulata*				
O. granulata	24	P	GG	Asia
O. meyeriana	24	P	GG	Asia

* domesticated species, A: annual, P: perennial, A/P: medium,
A-P: differenciation from perennial to annual.

Conclusion

R. x brachyceras is a sterile perennial, but maintains itself by means of vegetative reproduction. The reproductive systems of weedy *Rorippa* species may indicate each characteristic in the colonizing strategy into their habitats such as paddy field. There are asexual reproduction systems (apomixes in a broad sense) only in perennial species with a few exceptions. Perennial *Mazus miquelii* and *Cardamine lyrata* reproduce many ramets by stolons, *C. sucutata*, *Coix lacryma-jobi* var. *lacryma-jabi*, the common type of *Agropyron tsukushiense* var. *transiens*, and *A. humidorum* by stump itself and culms, while annuals *M. japonicus*, *C. flexosa* and *C. impatiens*, ecological annual *Coix lacryma-jobi* var *ma-yuen* and the early ecotype of *A. tsykushiense* var. *transiens* do not asexually at all.

An annual is a plant that completes its life cycle and dies within 12 months, though the life span may overlap two calendar years because of wintering. There are two categories of annual life cycle, that which is ended more or less abruptly with flowering and seed set and that which has a potentially indefinite length of life that is usually ended within a year by a climatic event (Harper 1977). The former category is “true” annual in the strict sense, while the latter ecological annual and potential perennial. In the first category are many of the above grasses of Mediterranean climates and arable land. On this arable land, their life for an annual in a crop is relatively safe until harvest and they can use the period in continuous cycle of growth. However, the adaptive value of the second category has been hardly studied yet.

A comparative survey of numerous examples of herbaceous colonizing species revealed the existence of three major colonizing types (Ehrendorfer 1965): perennial polyploid, annual self-pollinated and annual diploid species in Dipsacaceae, Asteraceae/Anthemideae, and Rubiaceae/Rubioideae. These types represent different evolutionary strategies and are characterized by different patterns in respect to ecological position, vegetative and reproductive characters, genetic system, and population structure. Also, Stebbins (1950) recognized several types of fertilization and growth habit of certain Gramineae and pointed out three general characteristics. (1) Annual species are relatively uncommon in cool temperature regions and predominant in warm, dry ones, with seasonal rainfall. (2) The annuals are almost exclusively self-pollinated, while the perennial species may be either cross- or self-fertilized, depending on the species. (3) Among the perennial species those with rhizomes are almost exclusively self-incompatible and cross-fertilized, while the caespitose, “bunch-grass” types shown various degree of self- or cross-fertilization.

Baker (1965) described the characteristics and modes of origin of weeds as colonizing species. The weeds show an annual, rather than a perennial growth habit, a wide environmental tolerance during growth, and striking developmental homeostasis in the sense that they produce flowers and seeds successfully in a wide range of conditions. They also show plasticity in size in response to environmental variation. Then, he (1974) proposed the ideal weed characteristics as follows. (1) Germination requirements fulfilled in many environments. (2) Discontinuous germination (internally controlled) and great longevity of seed. (3) Rapid growth through vegetative phase to flowering. (4) Continuous seed production for as long as growing condition permits. (5) Self-compatible but not completely autogamous or apomictic. (6) When cross-pollinated, unspecialized visitors or wind utilized. (7) Very high seed output in favorable environment circumstances. (8) Produces some seed in wide range of environmental conditions, tolerant and plastic. (9) Has adaptations for short and long-distance dispersal. (10) If a perennial, has vigorous vegetative reproduction or regeneration from fragments. (11) If a perennial, has brittleness, so not easily drawn from ground. (12) Has ability to compete interspecifically by special means (rosette, choking growth, allelochemics).

Actually, in colonizing species, it is in phases of germination and seedling establishment that their success or failure is most critically determined. Besides, the survival value of germination polymorphism is stressed. The germination polymorphism occurs in the adaptation to various environmental conditions, i.e., light, temperature (Harper 1965; Cavers and Harper 1966; Shimizu and Tajima 1975).

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