Chapter 3. Evolution of the Poaceae

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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 C_4 photosynthesis seems likely to be due to dearth of CO_2 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 (crossability 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.

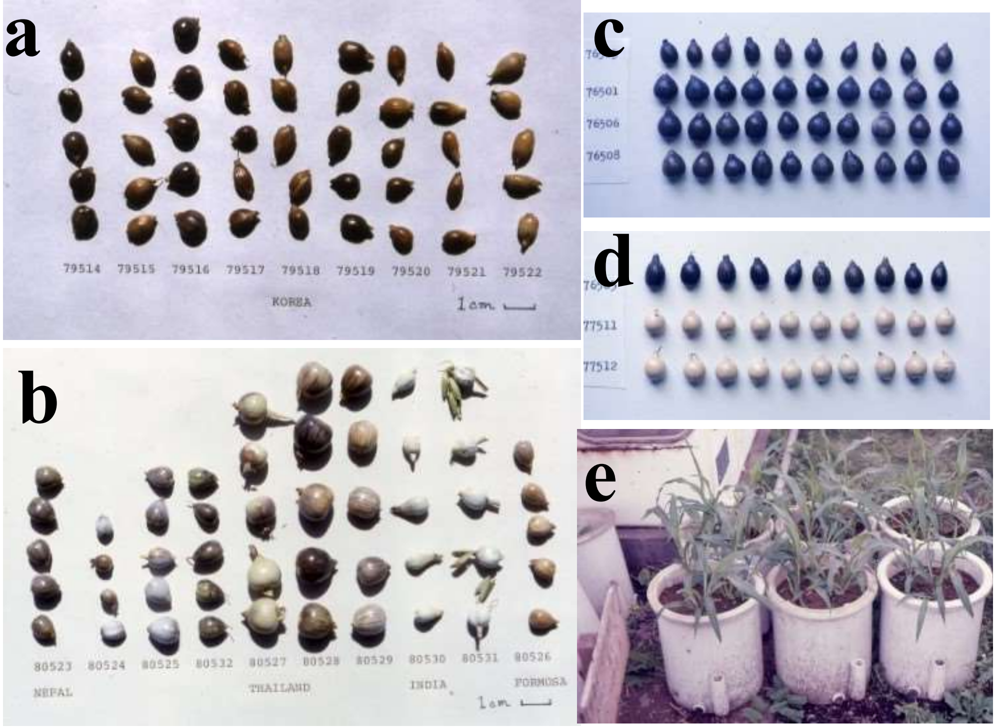


Figure 14. Morphological variation of bract sheath in *Coix lacryma-jobi*
a,b,c,d, bract sheath; e, var. *ma-yuen* (upper) and var. *lacryma-jobi* (below)

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.

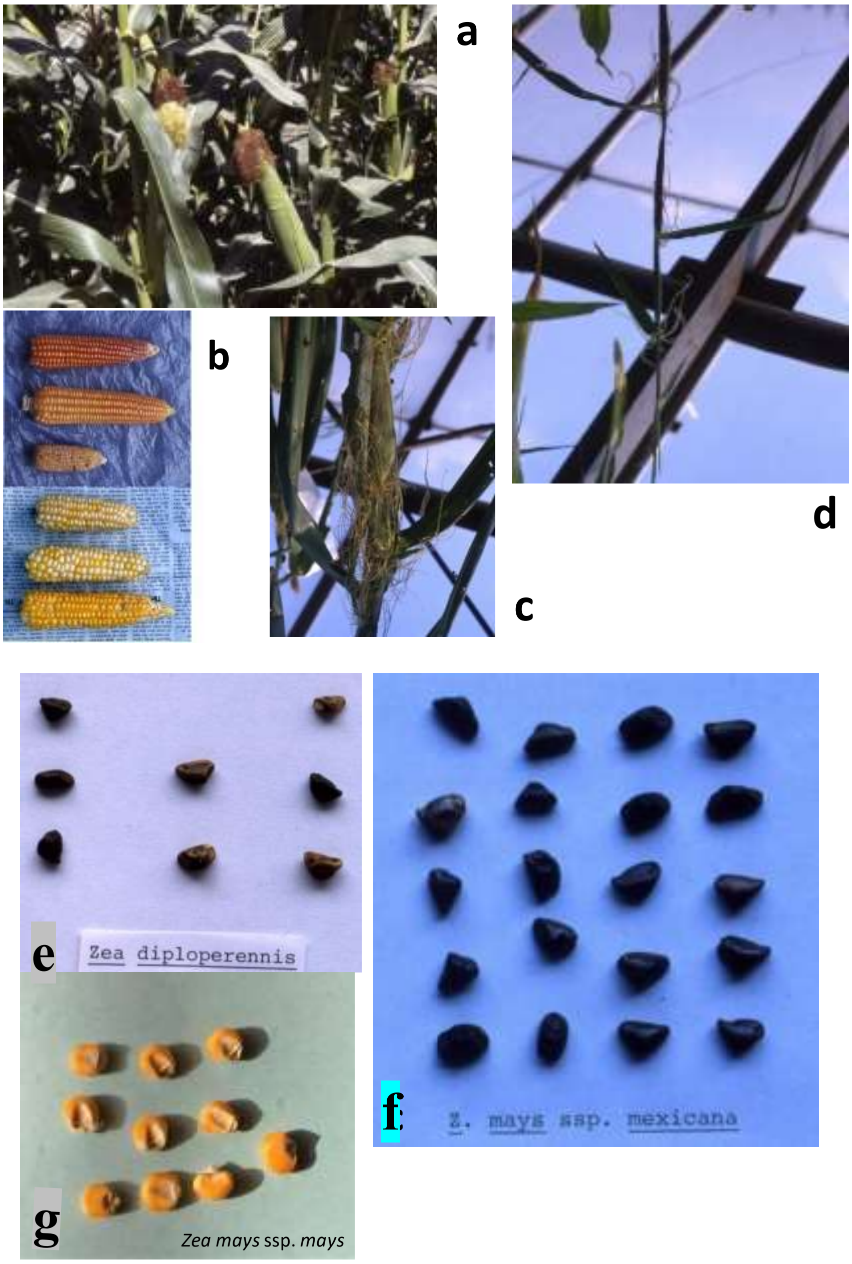


Figure 15. Ears and seeds of genus *Zea*

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.

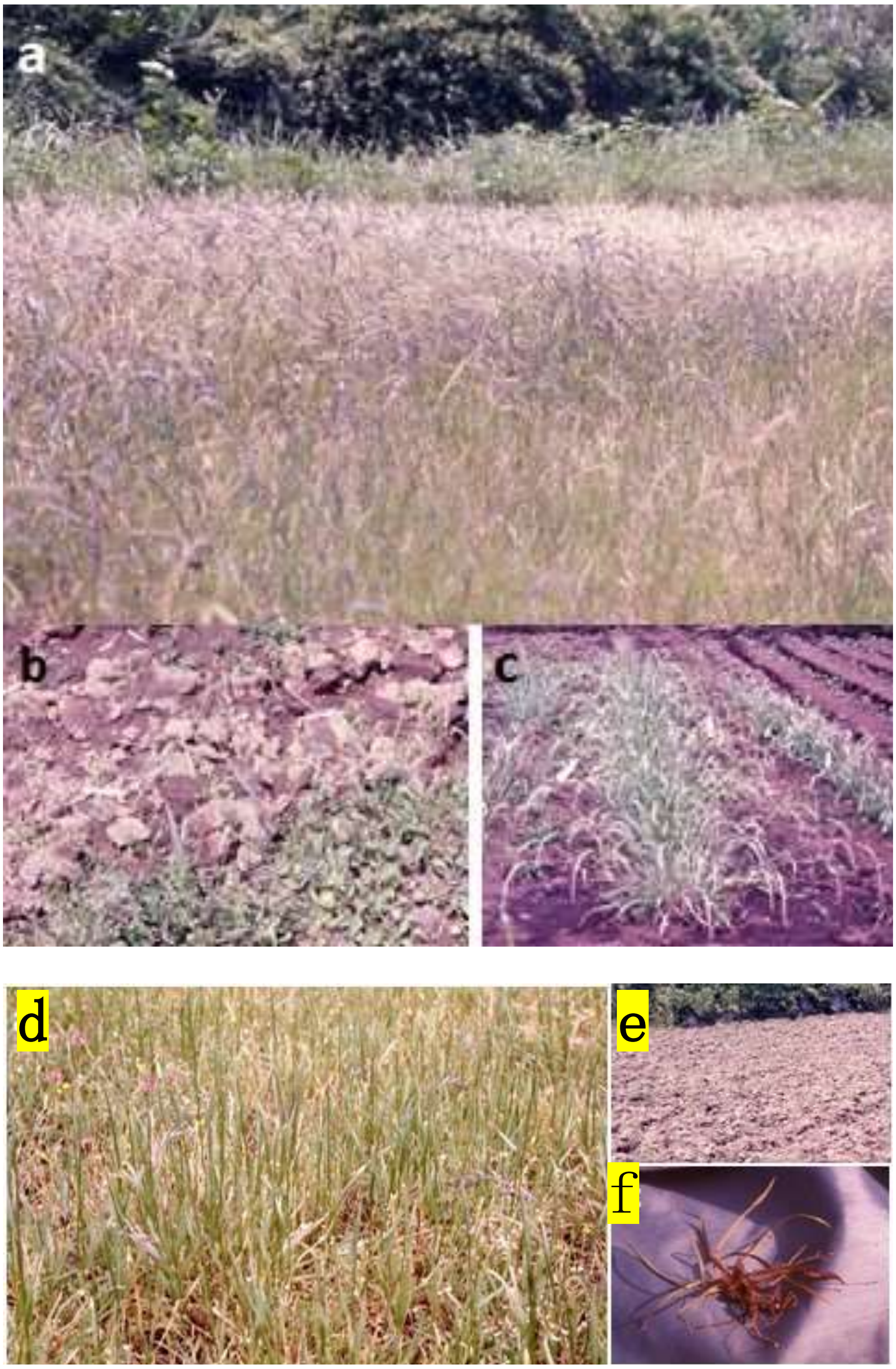


Figure 16. Weeds of genus *Agropyron*

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).

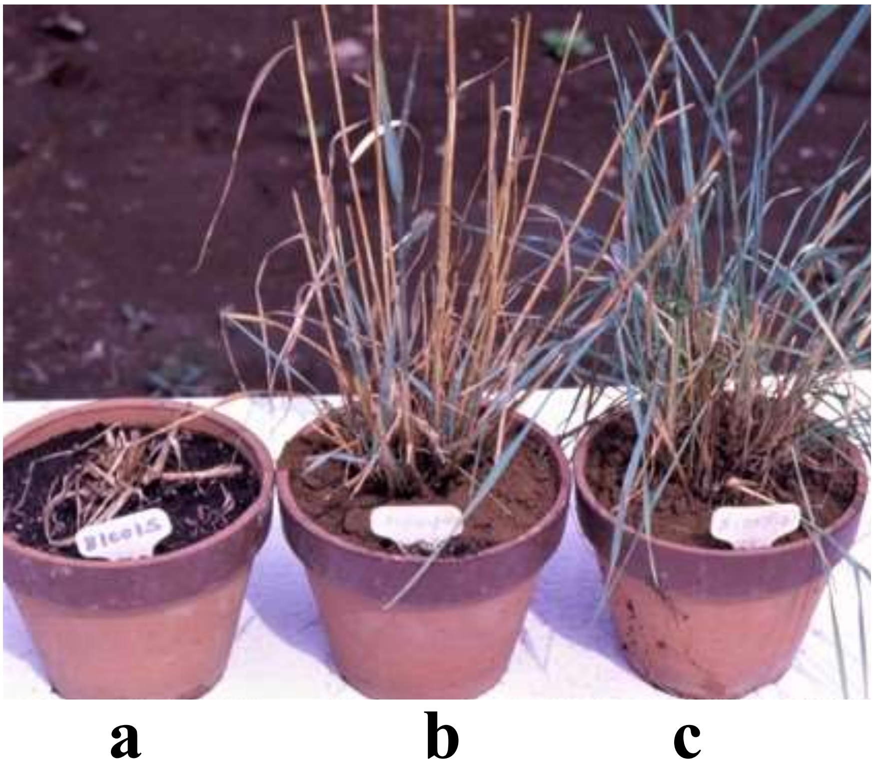
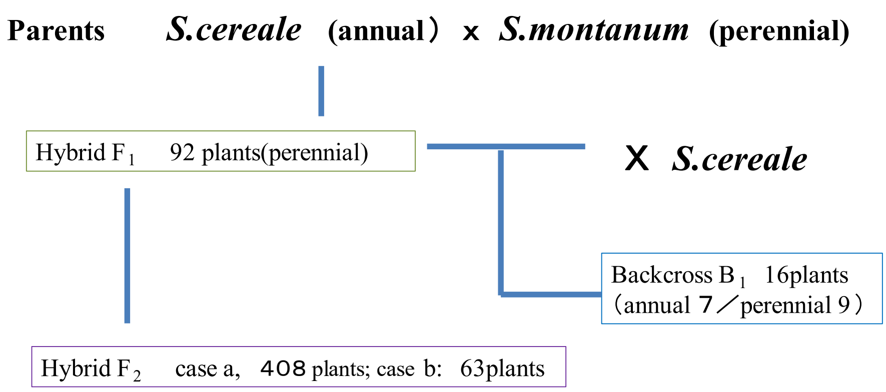


Figure 17. Hybrid F$_1$ (c; perennial) between *Secale cereale* (a; annual) and *S. montanum* (b; perennial)

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.

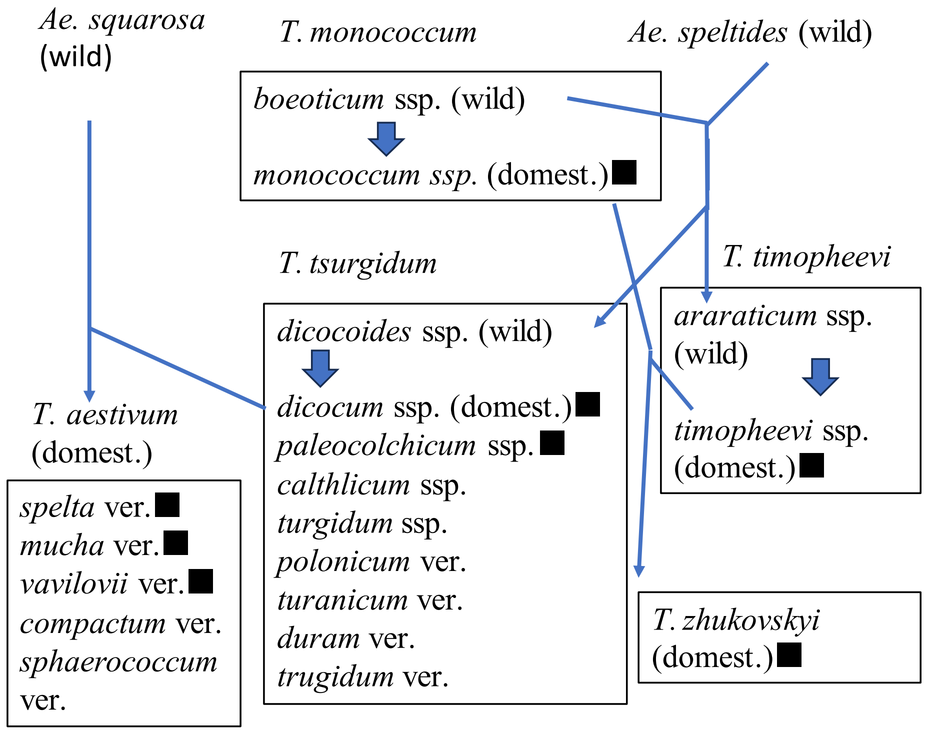


Figure 19. Origins and domestication of five groups in genus *Triticum*

→ 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.

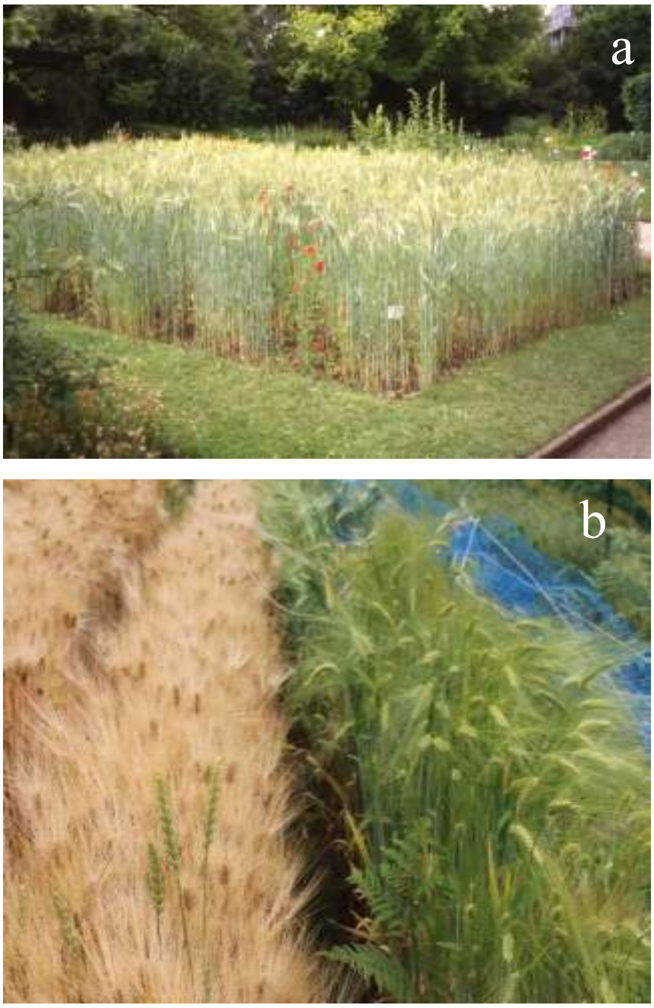


Figure 21. Wheat and Barley

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.

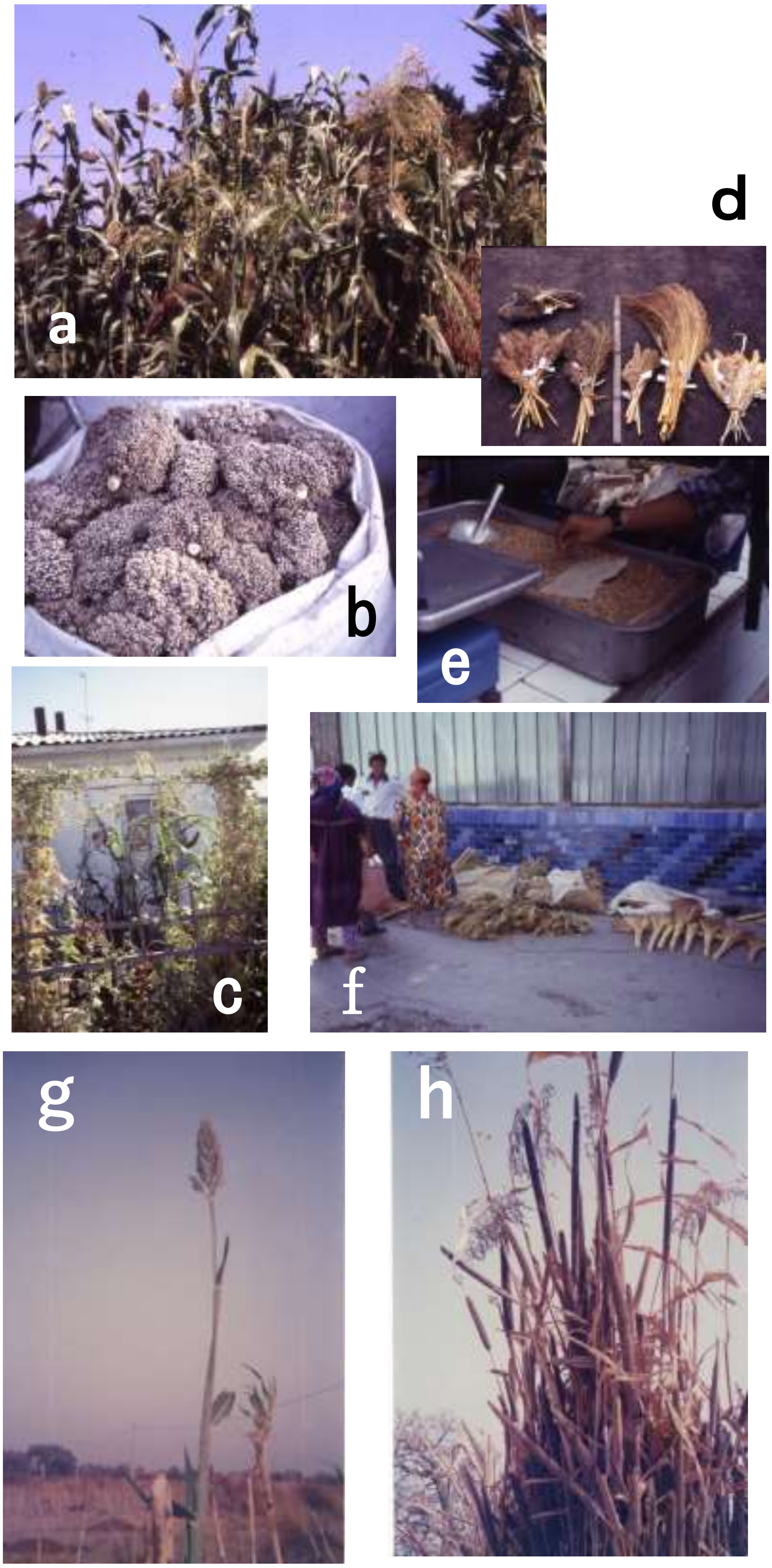


Figure 22. *Sorghum bicolor* in Central Asia and Africa

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.

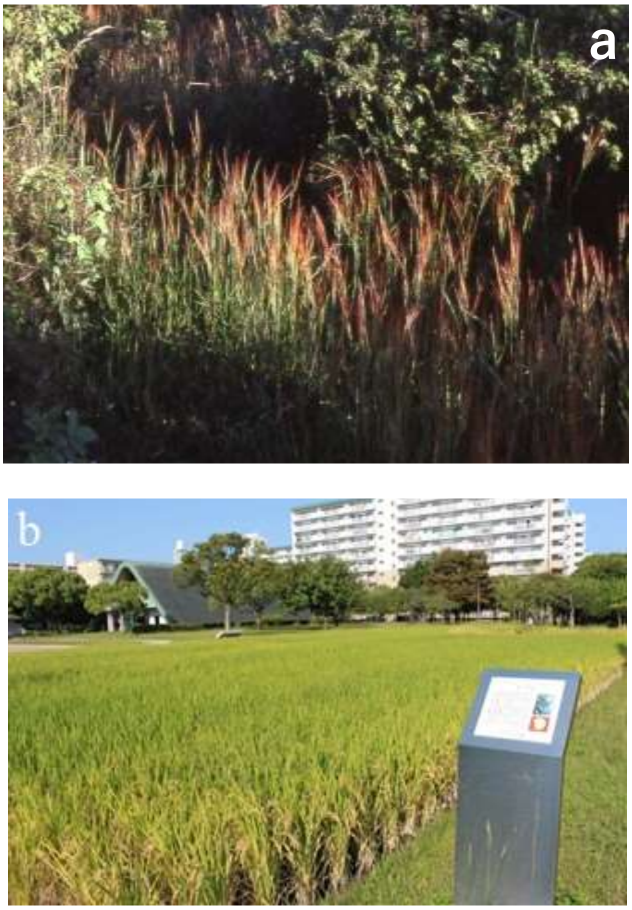


Figure 21. Rice paddy field

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).