Key Elements of Millet Ethnobotany

Origins and Distribution Across the Indian Subcontinent

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Photo; Transplanting finger millet on paddy field in South India

Contents

Preface

Throughout most of my career, I have focused on the domestication process and dispersal routes of grain crops, with a particular emphasis on millets within the Poaceae (syn. Gramineae) family. My research concerning plants in the Quaternary period is guided by four primary objectives. First, I aim to understand how humans have expanded and deepened their relationship with plants during the course of evolution. Second, I examine the historical processes involved in the development of agricultural civilization, tracing the steps from early pre-farming practices such as the use of fire, through the transition to farming and horticulture, and considering the role of wild animals in these systems. Third, I explore the future agricultural technology, especially the application of bioscience and information technology, in comparison with contemporary agricultural practices. Fourth, I seek to integrate foundational botany, subsistence strategies, and agriculture within the framework of ethnobotany as it relates to millets. Furthermore, I have recognized that the domestication process in Asia can be traced through distinct stages, beginning in wetlands, progressing through paddy field, and finally extending to upland fields.

A pertinent question arises: Why do we study millets, often referred to as “orphan crops” today? These species are also known as neglected and underutilized. However, Dr. Swaminathan (2022) has questioned the appropriateness of this terminology. In India, 2018 was celebrated as a special year for millets, and the Indian government proposed the International Year of Millets to the Food and Agriculture Organization. While initially planned for 2026, the United Nations (UN) rescheduled it to 2023 so that it would coincide with the UN Decade of Action on Nutrition (2016–2025), the UN Decade of Family Farming (2019–2028), and the UN Declaration on the Rights of Peasants (2018).

Today, not only millets but also numerous landraces of domesticated plants have vanished. Consequently, people have forgotten traditional knowledge systems related to subsistence, leading to the loss of biocultural diversity. I propose that we transition toward a civilization that values and sustains all organisms, in order to reevaluate and continue the foundational cultural complexes that include subsistence practices originating in the Jomon period, upland farming, and paddy field agriculture in Japan.

In the present era, the Anthropocene within the Quaternary, the global human population has surpassed 8 billion. Food sovereignty and security have become urgent concerns under the pressure of climate change. As the yields of major grain crops have reached their upper limits, it is imperative to avoid crises by cultivating a wider variety of grains and ensuring the stability of total grain yields.

My academic journey began with a graduation thesis in 1972 entitled “Anther culture of Triticeae,” followed by a master’s thesis in 1974 on the “Tillering of *Zea mays*,” and a doctoral dissertation in 1980 titled “Evolution from perennials to annuals in weeds.” Alongside these studies, I conducted extensive field surveys of millets. I visited numerous farmers in the Kanto Mountain area, with my research methods evolving from physiological and ecological genetics approaches to multivariate analysis of morphological characteristics in both field and greenhouse settings, as well as quantitative analyses of biological components.

Beyond Japan, I visited farmers and agricultural fields across the Indian subcontinent, Central Asia, and other regions to collect local grain seeds and gather information about cultivation, processing, and cooking methods. I then conducted statistical analyses of the resulting data. My approach was to integrate all research findings across disciplines, including ethnology, cultural anthropology, archeology, and linguistics, all based on botany of weeds, millets, rice, wheat, legumes, and tubers. While supported by many researchers, I carried out all research activities independently until my retirement.

Over a decade after retiring, I have authored five self-selected books, drawing on research data accumulated over more than 50 years. By integrating these findings, I examined the domestication process and dispersal routes of various crops. This methodology represents a progression from scientific analysis to integrated environmental studies. Through this comprehensive approach, I have been gradually come to understand the sequence from gathering wild grains, to pre-farming and semi-domestication, leading to the domestication process (botanical origins) and dispersal routes (geographical resources). I remain committed to advancing ethnobotany into an integrated field that encompasses the origins of agriculture and city-states, ethnic food cultures, and comparative studies of agricultural terminology. Nevertheless, the rapid advancement of research technologies and the proliferation of published work highlight the limits of individual inquiry.

This special issue comprises studies on the agricultural complex, domestication process, and dispersal of millets, particularly *Setaria pumila* (syn. *Setaria glauca*) and *Panicum miliaceum,* as opposed to major crops like rice, wheat, barely, and maize, with a focus on the Indian subcontinent. *Setaria pumila* is distributed only within a limited area of the Deccan Plateau (Kimata 2015a, 2015b), while *Panicum miliaceum* is found throughout Eurasia (Kimata 2015d), including the Indian subcontinent, and has recently spread to North America and Australia. The distinct distribution patterns of *Setaria pumila* and *Panicum miliaceum* are especially intriguing from environmental and historical geographical perspectives.

Acknowledgments

During my 50 years as a researcher, I have had the privilege of meeting many masters and friends who have enriched and expanded the scope of my work. I have also been fortunate to experience beauty of nature and kindness of people. As a botanist, my life has been greatly enhanced by the presence of beautiful flowers and the joy they bring.

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Several expeditions were conducted by Kyoto University, Tokyo Women's University, and Tokyo Gakugei University with support from both Japanese and Indian governments in the Indian subcontinent between 1983 and 2001.The author cordially thanks the Indian farmers for kind giving local varieties of millets; Prof. S. Sakamoto and Dr. Y. Ishikawa from Kyoto University; the late Professor H. Kobayashi for his excellent advice and unwavering collaboration during field surveys in 1985, 1987, and 1989; Dr. Y. Suyama of Tohoku University; Prof. I. Fukuda of Tokyo Women's University; and Dr. L. Kanhasuan of Phranakhon Rajabhat University, Thailand for their thoughtful

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Chapter 1 Ethnobotany and the Research Methods

Grain crops across the world

The seeds of Poaceae grain crops are predominantly non-toxic, with only a few exceptions. They are known for their nutrient-richness and long shelf life. Many wild grains from this family continue to be consumed today. Notable examples include *Dactyloctenium aegypticum* (an annual species found in the savanna regions of Africa), wild rice *Oryza rufipogon* (a perennial species in east and south India), and wild rice *Zizania aquatica* (an annual species in the Great Lakes regions of North America). Table 1 presents the domesticated grain crops, revealing a wide variety of species. While some have disappeared over time, others remain in the process of domestication. A new model describing the domestication process and dispersal routes will be introduced in Chapter 7, following a discussion of the hypotheses proposed by de Candolle (1886), Vavilov (1926), Nakao (1967), Sakamoto (1988), and Graeber and Wengrow (2021).

Grain crops domesticated in Africa are primarily annual C_4 plants, whereas those in Southwest Asia within the Triticeae tribe are annual C_3 plants. Grain crops domesticated from Central Asia, India, and East Asia are also predominantly annual C_4 plants. However, certain species, such as rice, include perennial plants that are cultivated as ecological annuals. Through artificial selection during domestication, these perennials have been transformed into ecological annuals. The annual growth habit has been a crucial trait throughout the domestication process.

Millet is a collective term referring to grain crops that exclude major grains like bread wheat, rice, and maize. According to FAOSTAT 2022 data, the total yield of grain crops was 3.9 billion tons, with maize accounting for 37.7%, rice for 25.3%, and bread wheat for 23.3%. Millets contributed 0.5 billion tons, representing 13.7% of the total yield.

Millets are characterized by numerous small seeds (caryopsis) attached to large panicles. They are primarily summer annuals, domesticated in savanna regions under tropical and subtropical climates, as well as in monsoon areas within temperate zones (Sakamoto 1988). These crops have adapted to climate changes associated with crustal deformation during the Quaternary period, maintaining local adaptability through high genetic variability and plasticity achieved by crossing with related weeds. Most millets are C_4 plants, which allows them to possess superior photosynthetic capabilities and produce high yields in semi-arid and mountainous environments.

Millets exhibit high overall biomass. Humans consume the seeds, while animals feed on the stems and leaves. Thus, millets serve as valuable crops for small farmers engaged in animal husbandry. Under harsh conditions across Afro-Eurasia, millets remain a staple food. Furthermore, their popularity is increasing among urban populations due to their health benefits and function as nutritious foods.

Table 1. Domesticated grains across the world

Scientific name	English name	Indiann name	Chromosome number	Grawth habit	Photosynthesis	Ancester	Geographical origin
Africa							
Sorghum bicolor Moench	sorghum	jowar	2n=20 (2x)	annual	C4	*S. bicolor* var. *verticillifolrum*	Africa
Pennisetum americanum (L) Leeke	pearl millet	bajira	2n=14 (2x)	annual	C4	*P. violaceum*	Africa
Eleusinne coracana Gaertn.	finger millet	ragi	2n=36 (4x)	annual	C4	*E. coracana* var. *africana*	East Africa
Eragrostis abyssinica Schr.	tef		2n=40 (4x)	annual	C4	*E. pilosa*	Ethiopia
Digitaria exilis (Kippist) Stapf.	fonio		2n=54 (4x)	annual	C4	wild	West Africa
Digitaria iburua Stapf.	black fonio			annual	C4	wild	West Africa
Brachiaria deflexa (Schumach) C. E. Hubbard	animal fonio			annual	C4	wild	West Africa
Oryza glaberrima Steud.	African rice		2n=24 (2x)	annual		*O. barthii*	West Africa
Europe from India							
Digitaria sanguinalis (L.) Scop.	mana grass			annual	C4		Europe from India
Phalaris canariensis L.	canary seed			annual			South Europe
Asia							
1. South west Asia							
Avena sativa L.	oat		2n=42 (6x)	annual	C3		South west Asia
Avena strigosa Schreb.			2n=14 (2x)	annual	C3		South west Asia
Avena abyssinica Hochst.			2n=28 (4x)	annual	C3		South west Asia
Avena byzantina C. Koch.			2n=42 (6x)	annual	C3		South west Asia
Hordeum vulgare L.	barley	jao	2n=14 (2x)	annual	C3	*H. vulgare* ssp. *spontaneum*	South west Asia
Triticum monococcum L.	small spelt		2n=14 (2x)	annual	C3	*T. monococcum* ssp. *boeoticum*	South west Asia
Triticum trugidum L.		aja	2n=28(4x)	annual	C3	*T. trugidum ssp. dicocoides + Aegilops speltoides*	South west Asia
Triticum aestivum L.	bread wheat	gehun	2n=42 (6x)	annual	C3	*T. trugidum* + *A. squarrosa*	South west Asia
Triticum timopheevi Zhuk.			2n=28 (2x)	annual	C3	*Triticum timopheevi* ssp. *araraticum*	South west Asia
Triticum zhukovskyi Menbde & Ericzjan			2n=42 (6x)	annual	C3		West Goergia
Seale cereale L.	rye		2n=14 (2x)	annual	C3	*S. montanum*	South west Asia
2. Central Asia							
Setaria italica (L.) P. Beauv.	foxtail millat	thenai	2n=18 (2x)	annual	C4	*S. italica* ssp. *viridis*	Central Asia/South Tianshan
Panicum miliaceum L.	common millet	cheena	2n=36 (4x), 40, 49, 54 (6x), 72 (8x)	annual	C4	*P. miliaceum* ssp. *ruderale*	Central Asia/South Tianshan
3. India							
Panicum sumatrense Roth	little millet	samai	2n=36 (4x)	annual	C4	*P. sumatrense* ssp. *psilopodium*	India/Decan Plato
Paspalum scrobiculatum L.	kodo millet	kodora	2n=40 (4x)	perennial	C4	wild	India/Decan Plato
Echinochloa flumentacea Link.	sawa millet	jangora	2n=54 (6x)	annual	C4	*E. colonum*	India/Decan Plato
Brachiaria ramosa (L.) Stapf.	browntop millet	korne		annual	C4	wild	Inndia/East Garts
Setaria pumila (Poir.) Roem. & Schult.	yellow foxtail mil	kolati	2n=18 (2x), 36 (4x), 72 (8x)	annual	C4	wild	India/Decan Plato
Digitaria crusiata (Nees) A. Caus	Khasi millet	raishan		annual	C4	wild	India/ Khashi Hill
4. South east Asia							
Coix lacryma-jobi var. *ma-yuen* (Roman.) Stapf.	Job's tears	gurya	2n=20 (2x)	perennial	C4	*Coix lacryma-jobi* var. *lacryma-jobi*	Zomia
5.China							
Oryza sativa L.	rice	dhan	2n=24 (2x)	perennial	C3	*O. rufipogon* L.	China/ Pearl river
Echnochloa oryzicola Vasing.			2n=36 (4x)	annual	C4	wild	China/ Yunnan
Podiopogon formosanus Rendl				perennial		wild	Formosa
Fagopyrum esculentum Moench	buckwheat		2n=16 (2x)	annual	C3	*F. esculentum* ssp. *ancestrale*	South west China/Yunnan
Fagopyrum tartaricum (L.) Gaertn.	Tartary buckwheat		2n=16 (2x)	annual	C3	*F. tartaricum* ssp. *potanini*	South west China/Tibet
6.Japan							
Echinochloa utilis Ohwi et Yabuno			2n=54(6x)	annual	C4	*E. crus-galli*	North Japan
America							
Zea maays L.	maize	makai	2n=20 (2x)	annual	C4	*Z. mays* ssp. *mexicana*	Meso America
Panicum sonorum Beal.	saui			annual	C4	*P. hirticaule*	Mexico
Zizania aquatica L.	wild rice		2n=30	annual		wild	North America, Canada
Bromus mango E. Desv.				annual/perennial		wild	South Chile, South Argentina
Amaranthus hypocondriacus L.			2n=32, 34 (2x)	annual	C4	*A. cruentus* (*A. hybridus*)	Andes
Amaranthus acaudatus L.			2n=32, 34 (2x)	annual	C4	*A. cruentus* (*A. hybridus*)	Andes
Chenopodium quinoa Willd.			2n=36 (4x)	annual	C4	*C. quinoa* ssp. *miilleanum*	Andes

The concept of millet is commercially ambiguous in Japan. Herein, the term "millet" is used in its narrow sense (Table 2), rather than adopting the broader commercial definition.

Table 2. Millet-related terminology

Difinition	Explanation
Strict definition	Millet is the collective term to the grain crops without major grains such as bread wheat, rice and maize.
	Numerous small seeds (caryopsis) attached to a big panicle, mainly summer annuals which had been domesticated in savanna area conditioned under the tropical/sub-tropical zones, or in monsoon area under the temperate zone
Small millets	Foxtail millet, common millet, finger millet, and so on. except large seed millets, i.e., sorghum, pearl millet and Yob's tears.
Broad definition	Millets and pseudocereals including *Fagopylum* ssp., *Amaranthus* ssp,, and *Chenopodeum* sp.
Loosely difinition	Grain crops except major grains such as bread wheat, rice and maize. Recently, barley, rye, oats, or reddish/purple rice, sesame, perilla, mung bean etc. have been added comarcially.

Research Methods and Materials

Botanical Approaches

In the study of plant domestication, botany is regarded as a central discipline, as highlighted by de Candolle (1883), who emphasized integrating diverse domains, such as archeology and linguistics, into botany. De Candolle meticulously described each crop and underscored the significance of annual species, which played a pivotal role for ancient people due to their ease of cultivation. Most key domesticated plants belong to the Poaceae, Fabaceae, and Brassicaceae families. To accurately determine the geographical origins of domesticated plants, it is essential to investigate their wild relatives. Botany, therefore, serves as a powerful tool for clarifying the botanical origins of these crops, particularly given the gradual onset of farming over extended periods.

Vavilov (1926) contributed to this field by researching the botanical origins and geographical sources of domesticated plants using the differential phytogeographic method. Kihara (1954) advanced the understanding of bread wheat through genome analysis on Triticeae, elucidating its botanical origins. Building on de Candolle’s methodology, Nakao (1967) proposed concepts regarding botanical origins and geographical resources, demonstrating broad conceptual thinking. Nakao also expanded these theories, introducing ideas such as the “Evergreen broad-leaved forest culture,” in collaboration with Ueyama and Sasaki (1983).

Sakamoto (1988) shifted his research focus from the phylogenetics of Triticeae to millet domestication after an inspiring experience eating *injera* in Ethiopia. I became his student around 1970, subsequently studying the agricultural complex of millets in Japan and the Indian subcontinent.

Modern Ethnobotany

Cotton (1996) described ethnobotany as a diverse field that investigates all aspects of the reciprocal interactions between plants and traditional societies. Its multidisciplinary nature encompasses areas such as ethnoecology, traditional agriculture, cognitive ethnobotany, material culture, traditional phytochemistry, and paleoethnobotany. Applied research in ethnobotany includes economic botany (agriculture, crafts, pharmaceuticals) and ecological domains (flora management, biodiversity, human ecology). The discipline also highlights the importance of environmental laws, learning principles, and practical engagement with the environment. Ethnobotanical research methods draw from cultural anthropology, ethnology, and botany.

In my own research, I have greatly respected Nakao’s contributions, particularly the concept of the basic agricultural complex (1966, 1967), and have adopted it as a central framework for studying millets and environmental learning. However, I have consciously avoided adopting other influential hypotheses, such as the “Evergreen broad-leaved forest culture” and Yanakita’s “Rice-growing single ethnic group theory.” Following Dr. Sakamoto’s advice, I refrained from allowing prevailing hypotheses to shape my papers, opting instead to rely solely on my own data and findings.

Ethnobotany employs natural scientific methods, prioritizing direct accounts from farmers and firsthand observations in their fields. Personal experiences within the natural and social environments of villages are invaluable. My research included cultivation tests, biological experiments, and observations using seeds and herbarium specimens. This approach underpins my intent to develop a new model for domestication processes and dispersal routes.

Archaeological and Historical Perspectives in the Holocene and Quaternary

Investigations into domestication processes and the dispersal of crops are conducted not only within geographical contexts but across historical periods. Utilizing background materials from these eras is essential. While I have not directly examined or analyzed fossils or artifacts from historical sites, I have visited numerous museums and historical locations. My research has also involved reading archeological literature and engaging directly with many archeologists in Japan and the United Kingdom.

Ethnographic Resources in Millet Processing and Cooking

Millets, unlike other major crops, have rarely been discovered in archaeological excavations, and ancient documentary evidence about their use is limited. To address gaps in understanding their domestication and dispersal routes, field research data derived from ethnology and cultural anthropology must be investigated. These disciplines help elucidate the journey of millets from their cultivation to consumption—a process described in the framework of the basic agricultural complex (Nakao 1966, 1967). This approach encompasses all steps “from seeds to stomach,” including cultivation methods, processing and cooking techniques, food culture, and agricultural rituals.

Comparing the origins and dispersal of grain crops with cultural history reveals significant patterns. For instance, varieties of millet with glutenous starch have been widely distributed throughout East Asia, including Japan, but have not spread westward. These varieties disappeared en route to India, largely because Western populations did not prefer their taste.

Bread, made from bread wheat flour, exemplifies a processed food that spread from the Middle East both eastward and westward. Boiled rice originated in China and moved westward, while pilaf—a rice dish—spread from Central Asia toward the west and south. Maize, introduced from America to Europe after the 15th century, became incorporated into traditional dishes such as *polenta* in Italy or ugari in Africa, often replacing common millet or foxtail millet as the primary ingredient. It is important to carefully consider processing and cooking methods to distinguish between old and new culinary traditions.

The victor group had high-yielding grain, such as bread wheat, often supplanted traditional crops like einkorn and emmer wheat. When these groups assumed power, they frequently discriminated against indigenous crops favored by previous populations. Nevertheless, indigenous groups continued cultivating these neglected crops, relying on them for survival under harsh and impoverished conditions (Scott 2017). Thus, traditional crops have persisted for millennia, remaining integral to daily life. According to Johonson (1992), both dominant and traditional crops hold importance: bread wheat, rice, and maize became commodities and taxable goods for ruling groups, while crops like millets remained vital for sustaining indigenous communities.

For example, those classic cases of the foods for the victor were explained below. The white bread made from fine wheat powder was luxury food for such ruler groups as a king, nobility and priest in Middle Ages. The white wheat bread was a special food of God. Common people and famers had used brown bread (*maslin* mixed with rye). Farmers had grown bread wheat as a tax for the king/state but they had not allowed to bread wheat (Clifton and Stacey 1977).

Linguistic Analysis of Vernacular Millet Names and Processing and Cooking Methods

Although I made efforts to learn local languages, English served as the common language among researchers and local people due to the multitude of languages spoken. Nevertheless, communication sometimes involved double or triple translations between English and local languages. Researchers gathered knowledge on cultivation, processing and cooking directly from local farmers, who demonstrated their methods and wrote vernacular names of crops and foods in English characters for us. To ensure accuracy, these names were cross-checked with restaurant menus and cookbooks.

The integration of linguistic analysis into crop dispersal studies gained momentum after Bellwood and Renfrew (2002) proposed the "language/farming dispersal hypothesis," prompting researchers to combine linguistics, archaeology, genetics, and other disciplines. Further linguistic insights were drawn from works by Ohno (2000, 2004) and Southworth (2005).

Two important conceptual distinctions should be highlighted. First is the difference in terminology: "origin" refers to the domestication of plants from ancestral species through interactions between humans and plants, while "resource" pertains to farming activities within a specific geographical area (Tanaka 1975). The onset of farming was a gradual cultural process, ultimately leading to the formation of city-states and the establishment of agriculture by helots over several millennia. Second, there is a distinction between "farming" (subsistence activities) and "agriculture" (industrial-scale production), which is why the term "Agricultural Revolution" is used, rather than "Farming Revolution."

Field Research in Mountainous Villages: Cultural Anthropology

We conducted cultural anthropology field research alongside botanical experiments, surveying traditional farmers who cultivate various types of millet in the foothills and valleys of mountainous and hilly regions. We directly interviewed hundreds of farmers about their cultivation methods, processing, and cooking practices, and collected local millet seeds for study and conservation.

Our team traveled extensively throughout Japan, from Okinawa to Hokkaido, the Indian subcontinent, Central Eurasia, and other regions, collaborating with regional agricultural organizations and councils, including the National Bureau of Plant Genetic Resources, Indian Council of Agricultural Research, All India Millet Improvement Project, Pakistan Agricultural Research Council, Plant Genetic Resources Laboratory, and National Agriculture Research Center. Unlike typical anthropologists, we did not reside in a single village but covered broad areas.

Between 1983 and 2001, I joined six millet expeditions, collecting numerous varieties and related species from hundreds of farmers across villages and fields (Table 3). The primary focus was southern Himalayas and Western and Eastern Ghats in the Indian subcontinent. Fieldwork included travel by car, train, plane, and on feet (Figure 1), particularly in states such as Karnataka, Andhra Pradesh, Tamil Nadu, Maharashtra, Telangana, Maharashtra, Madhya Pradesh, Orissa, Chhattisgarh, Jharkhand, West Bengal, Bihar, Uttar Pradesh, Uttarakhand, Himachal Pradesh, and Jammu and Kashmir in India, as well as the North–West Frontier in Pakistan and Eastern Nepal. Intensive studies were carried out in Orissa (1987, 2001) and in Karnataka and Andhra Pradesh (1996, 2001).

Table 3. Millet research expeditions across the Indian subcontinent between 1983 and 2001

Year (month)	Locality	Research Team
1983.9-11	Nepal, India (Hariana)	The Japanese Scientific Expedition for Nepalese Agricultural Research
1985.9-11	Pakistan (Northwest province), India (Karnataka, Andhra Pradesh, and Tami Nadu)	Kyoto University Scientific Expedition to the Indian Subcontinent
1987.9-11	India (Jammu and Kashmir, West Bengal, Orissa, and Assam), Pakistan (Sind)	Kyoto University Scientific Expedition to the Indian Subcontinent
1989.9-10	Pakistan (Azad Kashmir), India (Karnataka, Madhya Pradesh, and Maharashtra)	Kyoto University Scientific Expedition to the Indian Subcontinent
1996.9~97.6	India (Karnataka, Andhra Pradesh, Tamil Nadu, Orissa, Himachal Pradesh, and Utter Pradesh)	Research abroad supported by Japanese Government, University of Agricultural Sciences at Bangalore
2001.9-10	India (Karnataka and Orissa)	Tokyo Gakugei University Scientific Expedition to the Indian Subcontinent

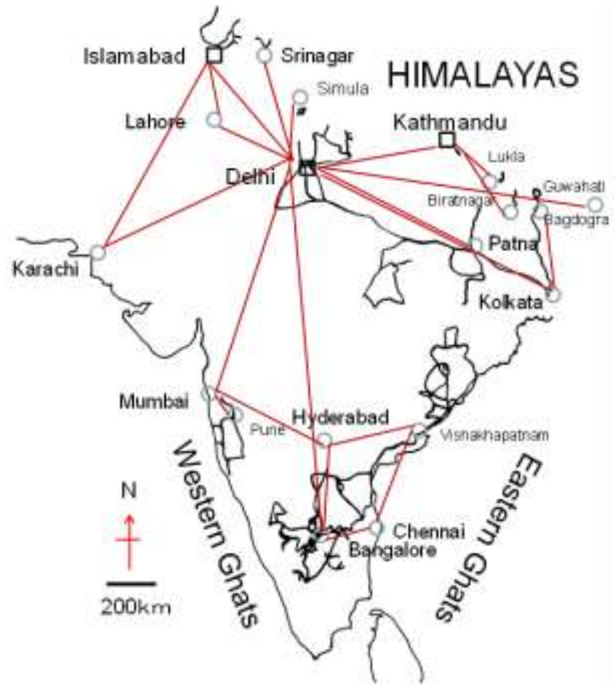


Figure 1. Expedition routes in the Himalayas, and Western and Eastern Ghats

Research Study Procedures

Early scholarly approaches to the origins of domesticated plants varied significantly. Some, like Frazer (1911) and de Candolle (1883), relied on extensive literature reviews, drawing specifically from numerous books to formulate their hypotheses. In contrast, researchers such as Vavilov (1926) and Kihara (1954) emphasized fieldwork and botanical experimentation, basing their theories on direct observations and experimental results. Sakamoto (1988) continued this strategy, conducting field research and eco-genetical experiments with numerous accessions, including domesticated plants and related species, all collected for use as experimental materials.

A notable example comes from the savanna regions of Africa, where a diverse range of wild Poaceae species were gathered for grain food—32 species in total, spanning *Aristida* (1), *Becheropsis* (1), *Brachiaria* (4), *Cenchrus* (2), *Dactyloctenum* (1), *Digitaria* (1), *Echinochloa* (3), *Eleusine* (1), *Eragrostis* (2), *Eriochloa* (1), *Hyphrrhenia* (1), *Latipes* (1), *Loudetia* (1), *Oryza* (1), *Panicum* (3), *Paspalum* (1), *Saccolepis* (1), *Setaria* (2), *Sorghum* (1), *Sporobolus* (1), and *Urochloa* (2) (Nakao 1967). While grasslands and wetlands are predominated by perennials, annual species grow in savanna regions. In fact, the first stage of pre-farming begins by gathering annual grains. This is followed by semi-domestication activities—cultivation, transplanting, weeding, plowing—and, ultimately full domestication involving sowing, harvesting, processing, and cooking. Although perennial Poaceae are also gathered, their domestication has largely ceased; for instance, while 35 species of *Setaria* are perennials found in Africa, none have been domesticated (Nakao 1967). This underscores the importance of annual plants in domestication.

At the outset of my research plan, I conducted comparative studies of annuals and perennials, compiling lists of these plants within the same genera using botanical encyclopedias. Selected genera for studying the evolution from perennial to annual included *Mazus*, *Cardamine*, *Rorippa*, and *Secale,* while *Agropyron*, *Coix*, and *Oryza* were chosen to explore ecological changes from perennial to ecological annual forms. Details of these comparative studies are presented in Chapter 2.

My subsequent research focused on the domestication process and dispersal routes of Common millet (*Panicum miliaceum*), an ancient, domesticated millet in Eurasia (Chapter 3). I also conducted comparative studies on Indian-original millets, encompassing morphological and ecological characteristics, biological component analysis, and genetic analysis through artificial outcrossing (Chapter 4). By learning new experimental techniques, I was able to analyze each species at the biological level, from population genetics to molecular analysis (Chapter 4).

Shifting focus to food processing and cooking methods, I studied the characteristics of agricultural resources and their dispersal within local communities (Chapter 5). Ultimately, I proposed a new model for the domestication process and dispersal of millets and grain crops in the Indian subcontinent (Chapter 6).

Conservation activities of biocultural diversity

I have organized agricultural complex materials and made them available on my website, which is registered with the National Diet Library {http://www.ppmusee.org/goods.html and https://www.milletiimplic.net/index.html}.

Chomin Nakae (1847-1901) noted that most Japanese academics rely on imported and translated foreign books, as limited language proficiency makes translations comfortable to use. However, when translations are inaccurate, it becomes necessary to revisit the original texts. Conversely, Japanese works are rarely translated into foreign languages, leading to a preference for writing books and papers in English for international readers.

Guided by Nakao' conceptional ideas and Sakamoto' self-reliance, I have conducted numerous botanical experiments and traveled widely for over 55 years. In the Indian subcontinent, I participated in research teams from Kyoto University, Tokyo Women's Christian University, and Tokyo Gakugei University between 1983 and 2001. I also served as an overseas research fellow at the University of Agricultural Sciences in Bangalore, India (1996–1997), and later at the University of Kent (Canterbury, UK) and Royal Botanic Gardens, Kew (2005–2006) for material collection. After my retirement in 2014, I joined as a fellow of the Research Institute for Languages and Cultures of Asia and Africa at Tokyo University for Foreign Studies (2014–2019), where I studied Indian culture and archeology.

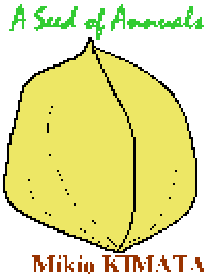
Throughout my career, I have emphasized the importance of inheriting biological diversity and traditional culture as an integrated cultural complex, especially through research on millet domestication process. Shiva (1993) insightfully wrote in *Monocultures of the Mind* that "Diversity as a way of thought as a way of life is what is needed to go beyond the impoverished monocultures of the mind," highlighting the decline in biocultural diversity.

We have undertaken several projects, including workshops and seminars on millet farming, and designated activities such as the Globally Important Agricultural Heritage Systems "Millet Street." The Plants and People Museum also returned local variety seeds to farmers who had lost them. In 2010, we presented a position paper, "People and Seeds for the Future: The importance of conserving plant seeds for the sake of bio-cultural diversity," to CBD/COP10 in Nagoya.

Following the Great East Japan Earthquake in 2011 and the Fukushima nuclear reactor accident, radioactive contamination threatened plant genetic resources. To protect them, I immediately transferred approximately 10,000 millet accessions to the Royal Botanic Gardens, Kew, UK.

My life's work has centered on the study, conservation, and popularization of millets. Despite this, Japanese society has not recognized the importance of millet, nor valued research on learning environments and biocultural diversity (Chapter 7). Many have lost their identity as self-sufficient farmers and become merely consumers, neglecting food security for monetary priorities. The "orphan millets" face deep-rooted prejudice, even in rural areas historically rich in millet cultivation. It is thus crucial to reconnect daily life with self-esteem and hope for the future. My wish is that everyone will reflect deeply on their families, local communities, and country, striving for happiness through pure, peaceful, and fulfilling lives. I have maintained relationships with a few intelligent farmers who remain dedicated to rural life.

Chapter 2 Plants and People in the Quaternary



Many people express curiosity regarding the ancestral species of domesticated plants, yet few truly understand the domestication process that unfolded between plants and humans. There is often limited awareness of the coevolutionary relationship that has shaped both. To address this gap, I conducted botanical experiments and field research focused on growth habits and reproductive systems—critical characteristics in the domestication process. These studies extended beyond the Poaceae family, encompassing additional genera for comparative analysis of growth habits and reproductive systems. These investigations ranged from ecological genetic studies to molecular analysis of biological components.

Comparative ecological genetics: Annuals and perennials

Nakao (1967) and de Candolle (1883) stressed that studying the evolution of annual plants is crucial for understanding the origins of domesticated plants. Their insights directly influenced my doctoral thesis (Kimata 1980), which explored the comparative ecogenetics of annual and perennial plants. Sakamoto's guidance led me to examine how annuals might have evolved from perennials.

According to the evolutionary timeline illustrated in Figure 2, C4 plants first emerged during the Tertiary era, approximately 7 million BP, followed by perennial herbs in the Neogene period. Annual herbs appeared later in the Quaternary, approximately 2.58 million BP. Annuals survived severe conditions—cold, heat, and drought—through seed dormancy. In response to environmental changes, plant reproductive systems diversified significantly. Synchronically, the ancestral genus *Homo* appeared, and gregarious animals adapted to and settled in grasslands.

Perennial species demonstrate considerable diversity in reproductive strategies: Perennials I are primarily cross-fertilized and self-incompatible species; Perennials II are cross-fertilized species or occasionally reproduce via parthenogenesis; Perennials III reproduce solely by parthenogenesis; Perennials IV display cross- and self-fertilization and are self-compatible. Annuals, evolved from Perennials IV are primarily self-fertilized, although cross-fertilization occasionally occurs. Annuals can produce numerous seeds. Table 3 compares the general characteristics of annuals and perennials. However, it is essential to recognize that individual species exhibit in wide range of habits in the following chapters.

Evolution from annual to perennial plants

Understanding the plant growth evolves from perennial to annual is important, as most cultivated are annual or annual-like. The reproductive systems of annual and perennial species generally differ (Baker 1955, 1959, 1974; Stebbins 1957, 1958, 1974; Ehrendorfer 1965; Harper

1967; Antonovics 1968; Harper and Ogden 1970; Kawano 1974; Jain 1976): annuals reproduce exclusively by seed (sexual reproduction), while perennials utilize both sexual and vegetative strategies. Annuals are often self-pollinated, whereas perennials are more often cross-pollinated. Notably, self-pollinating taxa are derived from outcrossing relatives, and annuals are derived from perennials.

It is generally thought that inbreeding and the resulting homozygous genotypes may sacrifice evolutionary capacity for change. However, another perspective suggests that the evolution of inbreeding (self-fertilization) is not merely accidental but may be favored by natural selection, as self-fertilizing species can have advantages over cross-fertilizing species under certain conditions.

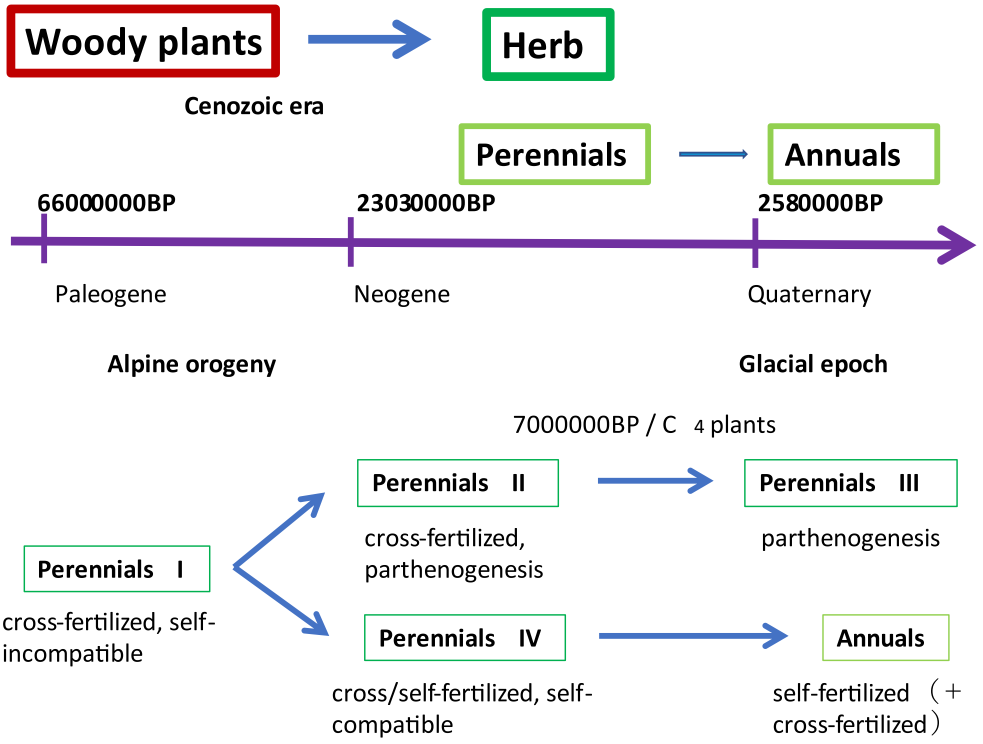


Figure 2. Phylogenetic evolution of herbaceous plants

Annual plants are self-fertilizers, producing many small, whitish flowers and numerous small seeds (Table 3). Self-fertilization reduces genetic variability, but polyploidy helps preserve biodiversity. Annuals are well adapted to colonize habitats disturbed by natural events or human activity. Their self-fertilization strategy supports their success as colonizers and pioneers. Most annuals utilize the C_4 photosynthetic pathway, allocating significant energy to seed production. Their phenotypes exhibit considerable environmental variations, which have been advantageous during domestication.

Conversely, perennials are predominantly cross-fertilizers and employ both seed and vegetative reproduction. They are generally diploid and utilize the C_3 photosynthetic pathway. Interspecific hybrids between annual and perennial species within the same genus are rare, but in experimental settings, the perennial trait is genetically dominant, while the annual trait is recessive. Moreover, *Oryza sativa*, *Coix lacryma-jobi* subsp. *ma-yuen*, and *Paspalum scrobiculatum* are botanically perennial, but have become 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

Throughout domestication, evolution has involved artificial and natural selection. For annual plants, key characteristics include reproductive systems (self-fertilization, cross-fertilization, or vegetative propagation), seed size and number, photosynthetic pathway (C_4 or C_3), and energy allocation, among others. The annual life cycle of grain crops is closely related to seed production (Table 4).

Compared with perennials, annuals do not undergo vegetative propagation, excluding rare exceptions like cleistogamy. They typically produce numerous small whitish flowers via sexual reproduction, often with limited pollen for self-fertilization. Annuals are predominantly self-fertilizing (sometimes cross-fertilize), produce numerous seeds, and can produce a large population from a single seed. Self-fertilization decreases genetic variability, whereas polyploidy increases and accumulates genetic diversity.

For example, the self-pollination rate of *Zea mays* is low (approximately 5%) due to anemophilous flowers and hermaphroditism. Species such as *Coix lacryma-jbi* and *Pennisetum americanum* are cross-fertilizers with protogyny, whereas *Sorghum bicolor* is a self-fertilizer. Typically, Brassicaceae plants are self-incompatible and cannot be pollinated by their own pollen. However, surprisingly, the self-pollination rate of *Oryza sativa* is nearly 100% despite its perennial nature.

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

	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, such as the savannah and Mediterranean areas, as well as in human-inhabited areas, where the environment is frequently disturbed during the growing season. In savannah climates, summer annuals are dominant, and local populations have domesticated various types of millet and constructed the Savannah Agricultural Complex. Conversely, winter annuals are dominant in Mediterranean climates, where the domestication of wheat and Triticeae species led to the formation of the Mediterranean Agricultural Complex. More recently, yearlong annuals have adapted to artificial environment in urban area. Although each annual plant completes its life cycle—flowering, fruiting, and dying—within one year, their populations persist year-round, exemplified by species such as yearlong annual, *Mazus japonicus*.

Perennials grow in stable, undisturbed habitats, such as forests, mires, and wetlands. These species reproduce vegetatively and sexually, often generating abundant pollen but fewer, larger, and more colorful flowers. Perennials can also include self-incompatible species and are predominantly diploid, producing relatively few but larger seeds.

C_3 plants perform photosynthesis exclusively through the carboxylic acid cycle, with the initial product being trimonosaccharid (3-sulfoglyceric acid). This category encompasses numerous species, including *Oryza sativa*, *Triticum aestivum*, *Glisin max*, and *Brassica napus*. Meanwhile, C_4 plants initiate photosynthesis via the C_4 pathway (dicarboxylic acid cycle) before transitioning to the carboxylic acid cycle. Approximately 20 families and 3000 species—including Poaceae, Cyperaceae, Amaranthaceae, and Chenopodiaceae—are C_4 plants, primarily inhabiting tropical and subtropical zones. C_4 plants exhibit higher photosynthesis rates and greater efficiency in water and nitrogen utilization compared to C_3 plants (https://www.jaicaf.or.jp).

Native annals account for over 40% of weed species in Japan (Table 5), with 344 species including prehistoric, naturalized plants (Kasahara 1974). Native perennials also represent approximately 40% of the weed population. Among naturalized species, annuals comprise approximately 15% while perennials make up approximately 6%. Notably, the proportion of naturalized annuals is 2.5 times higher than that of perennials. Summer annuals are commonly associated with weeds in rice paddy fields, whereas winter annuals are typically found in wheat fields. When newly emerging weeds invade disturbed habitats, annuals hold an ecological advantage, making them more likely to become naturalized weed species.

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)

Ancestral and related species of domesticated grain crops have grown near human habitats (Figure 3). For example, *Setaria viridis* is the ancestor of *S. italica,* and both species generate hybrids. *Setaria pumila* is the ancestral species of kolati, *S. pumila,* in Eastern India; *Coix lacryma-jobi* subsp. *lacryma-jobi* is the ancestor of 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 related to domesticated plants in non-boring sites.

Ecological genetics of the five genera

Most annual plants can produce numerous seeds through autogamy (Baker 1974). With self-fertilizers, a single individual can establish a colony even in temporarily disturbed habitats, facilitating long-distance dispersal (Baker 1955, 1959; Stebbins 1957, 1958; Antonovics 1968; Lefébre 1970; Jain 1976).

Perennial species, in contrast, are typically cross-fertilized and are generally polycarpic, meaning they live for more than one year. Annual species are monocarpic, completing their life cycle and dying within one year (Harper and White 1974; Harper 1977). Annuals reproduce predominantly by sexual reproduction via seeds, with few exceptions. Perennials utilize sexual and vegetative reproduction modes (Baker 1959; Harper 1967; Harper and Ogden 1970; Kawano 1974).

When comparing reproductive allocation, annuals invest a greater proportion of their dry matter into seed production. Conversely, perennials often allocate a significant portion of their reproductive resources to vegetative propagules or storage organs (Eherendorfer 1965; Harper 1967; Harper and Ogden 1970; Kawano 1974, 1975; Ogden 1974; Kawano and Nagai 1975).

The seasonal variation in population density of summer annuals has been investigated in conditions with and without winter annuals (Raynal and Bazzaz 1975). However, few studies have been conducted on sympatric habitats, where annual species coexist with related perennials.

To clarify the ecogenetic characteristics of annual species and their perennial relatives, comparative studies were conducted across seven genera: *Mazus* (Scrophulariaceae), *Cardamine* and *Rorippa* (Cruciferae), and *Agropyron, Coix, Secale,* and *Zea* (Gramineae). These studies provide critical insights into the ecogenetic underlying the origins of weeds and domesticated plants.

Comparison of life history strategies and reproductive systems between *Mazus japonicus* and *M. miquelii*, Scrophulariaceae

The family Scrophulariaceae comprises 210 genera and 3,000 species worldwide. There are ten species in the genus *Mazus,* three of which are found in Japan (Satake 1964). *Mazus japonicus* (Thunb.) O. Kuntze is an annual weed distributed throughout temperate and tropical regions from Afghanistan to China and Japan, within the Shino-Japanese floral region. *M. japonicus* was naturalized on the East Coast of North America approximately 100 years ago, while *M. miquelii* became naturalized approximately 50 years ago. The current distribution of these species in the United States is unknown (Michener, personal communication, 1977). *M. miquelii* Makino is a perennial weed found from Central China to southern Hokkaido in Japan. *M. faurei* Bon. inhabits southern Kyushu, Okinawa, and Formosa (Kitamura and Murata 1964). However, I have never observed these species in Kagoshima, Miyazaki, or Okinawa. *M. pumilus* (Burm. f) Steenis is a synonym of *M. japonicus*. Additionally, *M. goodcnifolium* (Hornrm.) Pennell and *M. quadriprotuberans* N. Yonezawa (1998) are present in Japan

M. japonicus (Thunb.) O. Kuntze was collected and observed in Koganei-shi and Kunitachi-shi, Tokyo, while *M. miquelii* Makino was detected in Hino-shi and Kunitachi-shi, Tokyo. Voucher specimens are deposited in the Herbarium of Tokyo Gakugei University (Figure 4). For comparison with *M. japonicus, Vandellia crustaceae* Bentham and V*eronica persica* Poir. were also studied ion in Kunitachi-shi. *M. japonicus* (annual) and *M. miquelii* (perennial) grow sympatrically in rice paddy fields. Their life history strategies were compared based on the relationship between reproductive systems and population dynamics in sympatric habitats (Kimata 1978; Kimata and Sakamoto 1979).

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

A close relationship between the number of blooming flowers and the number of visiting pollinators has been defined in *M. miquelii.* On sunny days, the peak in flower blooms aligns with the frequency of pollinator visits. The response time of stigma seismonasty in *M. miquelii* tends to be longer during the day than at night, while the recovery time tends to be shorter during daylight hours. This indicates that the stigma lobes of *M. miquelii* close more slowly and reopen more quickly during the day compared to nighttime. Since most pollinators are active during the day and stigma seismonasty ceases once pollination occurs, it is assumed that the stigma seismonasty in *M. miquelii* is an adaptation for cross-pollination by insects.

The growth habit of plants, whether annual or perennial, is typically observed through field observation. However, the growth habit can be determined only through experimental studies. For annual species, death occurs after flowering and fruiting without the formation of dormant buds. In the case of *M. japonicus,* plants survive low temperatures and frost but die following fruit production, confirming its annual growth habit. Field observations have revealed individuals at various growth stages throughout the year, with seed germination occurring successively from April to October and flowering following a similar pattern. In contrast, *M. miquelii* is perennial, producing numerous ramets through stolon formation. Flowering in *M. miquelii* is primarily influenced by temperature, with two observed flowering periods: in the spring (April–May), when plants produce asexually in the previous autumn bloom and produce abundant seeds, and from August to October, when fewer plants—germinated earlier in the year from May to June—flower atop stolons. During this latter period, most plants produce numerous asexual ramets.

The difference pollination systems of *M. japonicus* and *M. miquelii* are reflected in their seed production patterns. Capsules from self-pollinated *M. japonicus* contained more seeds with less variation in seed number compared to those from *M. miquelii.* Seeds of *M. japonicus* were also smaller and lighter, indicating a potential adaptation for effective dispersal. In contrast, *M. miquelii,* produced fewer seeds per capsule, with higher variability in seed number.

M. japonicus, characterized as a year-long annual, exhibits two main flowering seasons. Seed production occurs predominantly twice: in spring by winter plants and in autumn by summer plants. Within the winter population, plant sizes vary, influencing seed output. For example, a summer plant produced approximately 9,105 seeds, which was approximately three times the output of a small winter plant (2,929 seeds), but only about a fifth of the output from a large winter plant (51,241 seeds) that had germinated during summer. Averaging across individuals in winter populations, the seed count from summer plants is comparable to that from winter plants. Generally, the summer population of *M. japonicus* produces most seeds during autumn due to higher density, while the winter population produces many seeds in spring, leading to the germination of new summer plants.

M. miquelii has two flowering seasons: in spring (3,638 seeds) and autumn (60 seeds). Despite a high pollen fertility rate of 94.2%, seed fertility in autumn was only 16.7%, attributed to reduced pollen fertility under low temperatures. Consequently, spring seed production in *M. miquelii* is only approximately one-third that of *M. japonicus*.

While *M. miquelii*'s seed production was relatively low, the species compensates through asexual propagation via stolon formation. Plants formed by ramets can produce approximately 300 new ramets between May and October. In contrast, seed-derived plants contribute minimally to population expansion in the first year due to limited seed and ramet production.

Reproductive systems of two *Mazus* species

M. japonicus is a self-pollinated species, while the breeding behavior of *M. miquelii* is primarily characterized by cross-pollination with a low degree of self-incompatibility (Table 5). The differences in pollen size of the upper anthers and the pollen fertility of upper and lower anthers are not statistically significant between these two species, indicating these factors do not play a major role in their reproductive differentiation. However, the pollen fertility of the upper anthers in *M. japonicus* is significantly greater than that of the lower anthers (at the 1% significance level), suggesting its relevance to self-pollination within this species.

A notable distinction was observed in the proportion of under-lip length of stigma lobes between the species, with *M. japonicus* demonstrating markedly developed under-lip. The curved tip of the under-lip in *M. japonicus* facilitates self-pollination by partially enclosing the upper anthers. In contrast, *M. miquelii* does not exhibit extensive development of the under-lip of the stigma lobes, and its stigma shows seismonasty—a phenomenon documented in several plant families including Scrophulariaceae, Ranunculaceae, Pedaliaceae, Bignoniaceae, Capparidaceae, and Maryniaceae. *M. miquelii* in the Scrophulariaceae family serves as one such example. This trait is considered closely associated with insect-mediated cross-pollination and enhanced 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	year long annual
		germination, growth in summer, flowering/fruiting.	germination, growth in summer, flowering/fruiting .dead			
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

Annual plant species can be classified into three types based on their life cycle timing: summer annuals, winter annuals, and “year-long” annuals. *Vandellia crustacea* is a typical summer annual, as individuals of this species complete their life cycle from June to November. In contrast, *Veronica persica* serves as a typical winter annual, persisting from September through the following June. Distinct from these, *M. japonicus* demonstrates characteristics of summer and winter annuals, functioning as a year-long annual. Although each individual plant germinates and dies within a single year, the overall population is sustained throughout the year. All three species mentioned are annuals, even at the physiological level.

Veronica persica and *M. japonicus* display bimodal patterns of seed germination with two plant density peaks in November–December and March–April, and in November and June–July, respectively. A similar bimodal germination pattern is found in *Setaria faberii* Herm. which is thought to maintain two seed populations distinguished by their germination timing (Raynal and Bazzaz 1975). Although it remains unclear whether mortality in *V. persica* and *M. japonicus* is influenced by population density, it is evident that both drought and frost conditions have pronounced effects on their mortality rates.

The *M. japonicus* population has a long flowering period, which persists nearly year-round under both artificial and natural conditions, despite being an annual species. Summer plants produce more inflorescences than winter ones, resulting in most seeds being produced during the summer.

As outlined previously, *M. japonicus* primarily undergoes self-pollination, whereas *M. miquelii* largely relies on cross-pollination and also reproduces asexually through stolons. These differences in reproductive behavior are predicted to significantly impact their population dynamics. In their sympatric habitats—such as rice paddy fields—these dynamics are key for understanding why annual species often outcompete perennials in disturbed habitats. Annuals are superior colonizers due to their reliable seed production through self-pollination, allowing for rapid establishment of new populations (Baker 1955, 1959; Stebbins 1957, 1958; Antonovics 1968; Lefèbvre 1970; Jain 1976).

A model illustrating the population dynamics of *M. japonicus* and *M. miquelii* comprises four stages:

1) rice cropping: On the levee, the population density is approximately three plants of *M. japonicus*/m^2 and approximately 100 *M. miquelii* plants/m^2. In non-cultivated paddy fields, only approximately three *M. japonicus* plants/m^2 are present during winter.

2) Non-cropping (relinquishment): *M. japonicus* colonizes abandoned paddy fields with its seeds, while *M. miquelii* invades these areas from the levee via stolon growth.

3) Ill-drained abandoned paddy field: *M. japonicus* population decreases (approximately 50 plants/m^2 in the center) and *M. miquelii* increases (approximately 350 plants/m^2 near the levee), a pattern that may be inferred from the density of two species in areas near the creek.

4) Well-drained abandoned paddy field: *M. japonicus* population increases by seeds (approximately 350 plants/m^2 in the center), while *M. miquelii* decreases (a few/m^2 even near the levee).

Population dynamics in these two *Mazus* species are influenced by competition with other species, patterns of seed germination, and ramet (root) formation from stolon nodes in *M. miquelii.* The number of species on the levee is approximately twice that in fallow paddy fields, which restricts the increase in density for both *Mazus* species through seed germination. Light-dependent germinators face difficulties germinating in the shade of other plants on the levee, and even when germination occurs, seedlings may not survive. However, *M. miquelii* can reproduce on the levee via stolon propagation.

As grasses dominate the abandoned levee, only 29 *M. miquelii* plants/m^2 were recorded. In contrast, annual weeds dominated abandoned paddy fields, resulting in 108 *M. japonicus* plants/m^2.

A comparison of seed germination between the *Mazus* species reveals that *M. japonicas* can better germinate under a wider range of temperatures and lower soil moisture conditions than *M. miquelii*. However, *M. japonicus* seeds germinate more rapidly. For *M. miquelii,* rooting from stolon nodes requires less soil moisture (34.4%) than its seed germination (79.1%). Hence, *M. japonicus* is a more effective colonizer of disturbed habitats, while *M. miquelii* tends to be more abundant only on the relatively more stable levee habitat.

In winter plants of *M. japonicus,* seeds from the earliest (first-flowered) capsules germinate more rapidly than those from later capsules (fourth and eighth). Conversely, in summer plants, seeds from the eighth-flowered capsule germinate more rapidly than those from the first and fourth. This indicates significant variability in germination requirements among seeds, which likely contributes to the vigorous germination observed from May to July and the diversity in seed germination patterns.

Life history strategies of two *Mazus* species

The schematic life history models of *M. japonicus* and *M. miquelii* are illustrated in Fig. 5. *M. japonicus* is a year-long annual and self-pollinating species that reproduces through the production of numerous seeds, enabling it to thrive in a variety of habitats, including upland fields and roadsides. The species experiences two main periods of seed germination: the first occurs from April to June, and the second from September to October.

During the summer, the population consists of seedlings that originate from the seeds produced by water plants or from seeds that have remained dormant in the soil. These seedlings exhibit rapid growth in the summer, subsequently flowering, fruiting, and dispersing a large number of seeds between June and October. The autumn germination period leads to a winter population of seedlings, which develop from seeds of summer plants or those previously buried. These winter seedlings grow slowly, eventually flowering, fruiting, and dispersing seeds in the following April to June cycle.

Germination in *M. japonicus* is notably heterogeneous, resulting in significant age diversity within garden populations. Plant height, leaf number, and the number of inflorescences exhibit particularly high variability (c.v.), while the size of the largest rosette leaf is less variable. In summer, larger plants tend to flower and die by November, yet some smaller seedlings may grow larger and flower in the next spring.

M. miquelii is a perennial and cross-pollinating species that predominantly reproduces vegetatively via stolons and is typically found on the levees of rice paddy fields. Over its life cycle, wintered rosette plants flower, fruit, and disperse seeds in April–June, while also forming many ramets through stolon growth between May and October. These ramets continue to grow during autumn and winter, flowering in the next spring.

Seed and buried seed germination occur in May and June, leading to the formation of summer seedlings. These seedling grow throughout the summer, then flower, fruit, and disperse a few seeds from August to October. Similar to the spring cycle, ramet formation by stolons occurs again in September and October, with these new ramets growing during winter and flowering in the following spring.

The seasonal changes and allocation of total dry weight in *M. japonicus* reveal distinct differences between its summer and winter populations. Winter plants are characterized by the following three features; 1) lower crude reproductive efficiency; 2) store markedly more resources in their roots; 3) dry weight that is approximately three times that of summer plants at the end of the growing period. In contrast, summer plants continuously produce seeds with minimal root resource storage, while winter plant prioritize root storage and initiate seed production in spring.

In *M. miquelii,* the mother plant develops several roots and contribute to the elongation of stolons in May and September. Daughter plants (ramets) store significant resources in their roots during winter and began seed and ramet production in spring. However, the plants formed by seed produce few seeds (ca. 10 ramets) in autumn. The following spring, these ramets flower and produce many seeds and new ramets via stolons. However, few plants formed by seed are observed in natural populations. These plants, therefore, could play a secondary role in the life history strategy of *M. miquelii* two years post-germination, with genetic variability resulting from outcrossing increasing in their population.

The ability to store root resources during the winter is a shared trait between the winter plants of *M. japonicus* and the daughter ramets of *M. miquelii.* Moreover, all *Mazus* species except *M. japonicus* are perennials that grow in winter and flower in spring to early summer (Peking Institute of Botany 1975). *M. japonicus* may have evolved from a winter annual to a year-long plant due to reduced seed dormancy and earlier maturity, adapting to disturbed habitats.

These studies on *Mazus* species (Kimata 1978, 1979, 1986, 1991) contribute to resolving broader questions in plant life history strategy proposed by Harper (1967) and Kawano (1975) related to longevity, life cycle expression, reproductive energy allocation, and the balance between seed number and vegetative propagule production. The clear distinctions between the self-pollinated annual *M. japonicus* and the cross-pollinated perennial *M. miquelii* reflect the ecological and evolutionary outcomes of adaptation to their environment (Figure 5).

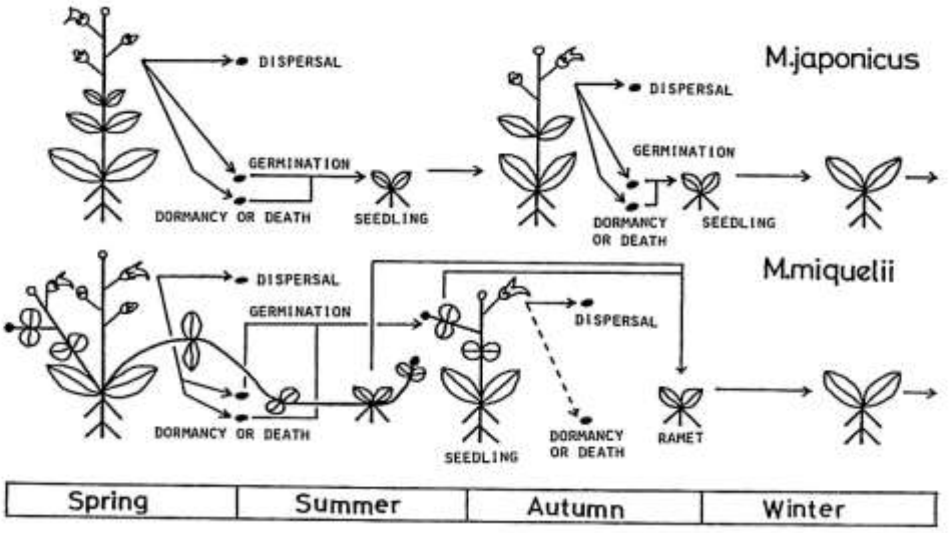


Figure 5. Schematic model of the life histories of *M. japonicus* and *M. miquelii*

⬬ seed; ○flower bud;●shoot apex.

These data on the life-history strategies of two *Mazus* species may offer additional evidence supporting the evolutionary trend in flowering plants from cross-pollinated perennials to self-pollinated annuals.

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. scutate,* and *C. lyrata* (perennials) were compared to provide further evidence for the evolutionary trend from cross-pollinated perennials to self-pollinated annuals. This study also investigated intraspecific differentiation between a year-long and winter annual types in *C. flexuosa* (Kimata 1983).

Seven strains of *C. 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 from shady gardens in Tokyo. *C. impatiens* L. was collected from a forest floor of *Cryptmeria japonica* D. Don in Yamanashi Prefecture. Five strains of *C. scutata* Thunb. were collected primarily from creeks in Tokyo, Shizuoka, and Kyoto Prefectures. Two strains of *C. lyrata* Bunge were found in paddy fields in Aichi and Mie Prefectures (Figures 6 and 7). For each strain, over 20 plants were collected, with 10 examined and the remaining were stored at the Herbarium of Tokyo Gakugei University.

C. flexuosa and *C. impatiens* are self-pollinated annuals, *C. sucutata* is a cross-pollinated perennial, and *C. lyrata* is a cross-pollinated perennial with self-incompatibility. Perennial species may exhibit either cross- or self-fertilization, depending on the species. The data support an evolutionary trend from cross-pollinated, self-incompatible perennials toward self-pollinated annuals via a self-pollinated perennial without self-incompatibility. This pattern is evident in these four *Cardamine* species.

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

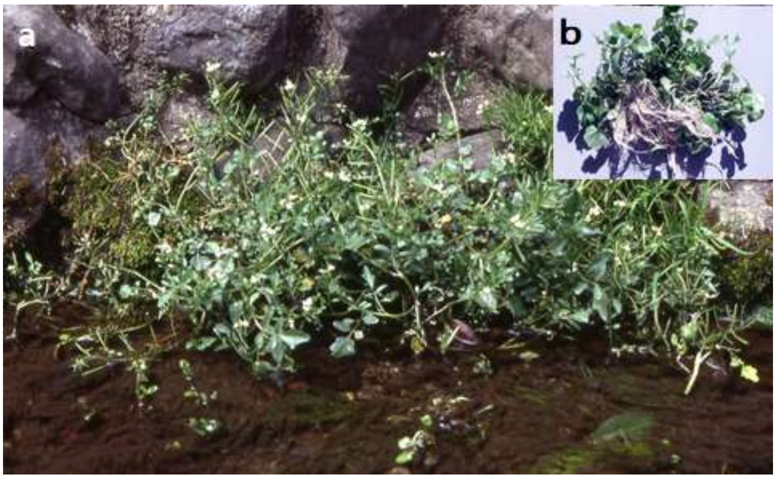


Figure 7. ***Cardamine sucutata* in stream**
a, Flowering; b, rosette

Self-pollinated annual species are often better colonizers in disturbed habitats, as massive seed production in the early stage of colonizing helps establish new populations (Stebbins 1958; Ehrendorfer 1965; Antonovics 1968; Lefèbvre 1970). Two subspecies of *C. flexuosa* are well adapted to these environments. *C. flexuosa* ssp. *flexuosa* flowers in February to April and yields numerous small seeds that fall near its own stump in paddy fields. These seeds are uniformly dispersed during cultivation in the fields, remain dormant condition until autumn, and then germinate.

Conversely, *C. flexuosa* ssp. *fallax* flowers from February to April and June to November. Its numerous seeds fall evenly within a certain distance, germinating between May and October after a short dormancy, leading to the establishment of summer and winter populations. This suggests that the two subspecies may employ different seed dispersal strategies. Friedman and Stein (1980) reported similar variability in dispersal strategies for the annual *Anastatica hierochuntica*, Cruciferae, with dispersal patterns influenced by rainfall and runoff.

C. impatiens, another self-pollinated annual species, has adapted to relatively stable habitats such as muddy forest floors and edges. Flowering occurs in March to May, producing numerous small seeds that disperse over short distances dues to the plant's erect growth form. Watkinson (1978) reported that seed dispersal distance in winter annual grass *Vulpia fasciculate* strongly correlates with the height of the infructescence. Similarly, *C. impatiens* with taller infructescence disperses seeds further than *C. flexuosa* and *C. scutate,* which have shorter infructescence. Germination of *C. impatiens* occurs in August after a brief seed dormancy.

Both *C. scutata* and *C. lyrata* are well-adapted for regularly cultivated, fertilized, and consistently muddy paddy fields. *C. scutata* flowers from February to April and August to September, producing rather numerous seeds that fall evenly into creek water nearby, and germinate immediately in May without dormancy. *C. lyrata* flowers in May, produces fewer seeds, which may be dispersed by floating on water (Figure 8). These seeds germinate in autumn after extended dormancy.

Overall, these results indicate that successful colonizers in disturbed habitats possess highly efficient seed dispersal mechanisms tailored to their specific environments.

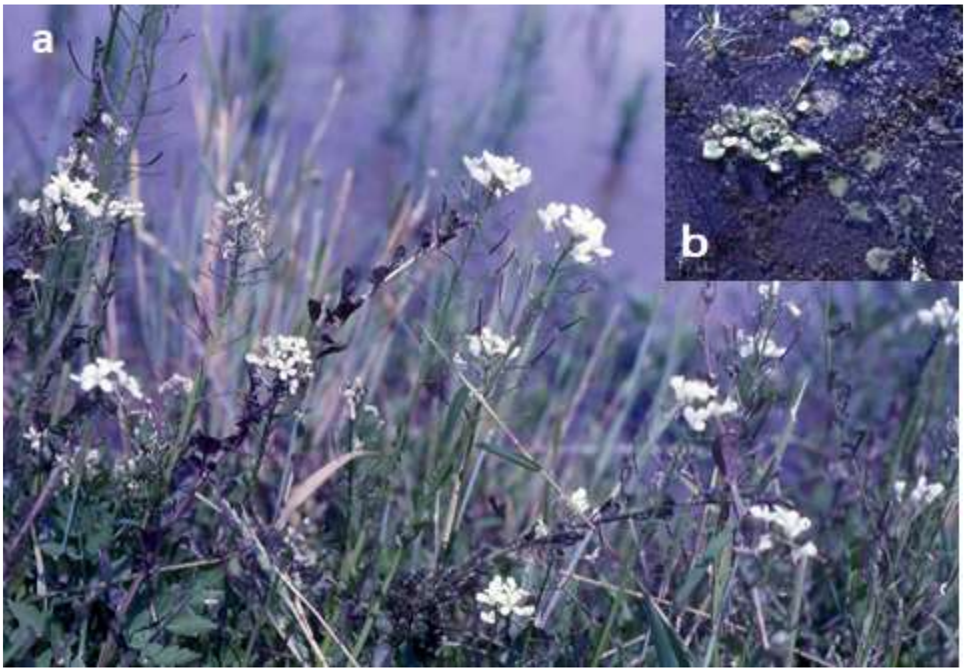


Figure 8. Cardamine lyrate in a paddy field

a, Flowering; b, ramets

The reproductive allocation of dry matter into sexual structures (e.g., seed) is considerably higher in annuals than in perennials. In contrast, perennial species tend to invest more heavily in asexual structures, including vegetative propagules and storage organs (Harper 1967; Harper and Ogden 1970; Kawano 1974, 1975). In the present study, the self-pollinated annual *C. flexuosa* allocates 26% of its total dry matter to siliques, which are sexual structures.

Conversely, the self-pollinated perennial *C. sucutata* allocates only 12% to siliques, but 48% to ramets, representing asexual structures, by the end of the growing season. The cross-pollinated perennial *C. lyrata* allocates less than 1% to siliques while directing 80% to stolons. Bell et al. (1979) assessed seasonal variation in biomass allocation across eight winter annual species, noting that roots contained 12–22% of total biomass until the late flowering, at which point root allocation declined; maximum reproductive investment ranged from 16 to 50% of total biomass. The winter annual *C. flexuosa* exhibited similar patterns in roots and silique allocation.

Rooting ability of stem segments varies among species: *C. lyrata* demonstrates a higher rooting rate (75.0%) than *C. flexuosa* ssp. *flexuosa* (17.5%) and *C. flexuosa* ssp. *fallax* (57.5%). In contrast, *C. scutate* exhibits a low rooting rate (5.0%), which may be closely associated with its limited capacity for vegetative reproduction. Notably, *C. lyrata* produces approximately 27 times more ramets than *C. scutate* (Table 6).

Table 6. Vegetative propagation of *Cardamine* species

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

The *Cardamine* species examined in this study can be clearly distinguished by various morphological features. Notably, the corolla of *C. lyrata* is approximately three times larger than those of other species, which may be closely related to its cross-pollination strategy.

Despite being capable of intraspecific crossing, *C. flexuosa* displays subspecies differentiation across several traits, including growing season, seed dispersal mode, and germination and flowering periods (Table 7). The subspecies *C. flexuosa* ssp. *flexuosa* typically forms large populations, but only in restricted habitats like fallow paddy fields. In contrast, *C. flexuosa* ssp. *fallax* can establish only small population (a few individuals per m^2) in spite of growing in diverse habitats, such as gardens, roadsides, and nurseries. This is likely because it produces fewer seeds and is only able to thrive in relatively moist microenvironments.

Table 7. Summary of *Cardamine* spp. reproductive systems

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

Crossability, seed germination rate, and pollen fertility of F₁ hybrids among six *C. flexuosa* strains from Japan and Nepal

C. flexuosa ssp. *flexuosa* is a winter annual subspecies, whereas ssp. *fallax* is classifieds as a year-long annual due to its capacity to establish populations in summer. Generally, species within the genus *Cardamine* undergo vegetative growth in winter and flower in spring. The year-long annual growth habit of *C. flexuosa* ssp. *fallax* might be derived from a winter annual form.

The experimental data and observations presented here on the life history strategies of *Cardamine* spp. provide further evidence for the general evolutionary trend from cross-pollinated perennial to self-pollinated annual breeding systems in flowering plants.

The term “ecotype” refers to an ecological sub-unit that emerges from the genotypic response of an ecospecies to a particular habitat (Turesson 1922, 1925). This basic biological entity is adapted to a range of habitats, each defined by particular environmental conditions, such as annual climate fluctuations, soil characteristics, and interactions with other organisms. Ecotypic differentiation is fundamentally a physiologic–genetic phenomenon (Clausen 1967; Armbruster 1985).

Among widespread species, ecogeographical differentiation is closely associated with factors such as population size, migration, genetic variation, natural selection, reproductive strategies, and mechanisms of isolation (Ehrendorfer 1968; Barton and Charlesworth 1984). Two primary patterns of intraspecific differentiation can be distinguished: allopatric and partly sympatric. Allopatric differentiation typically occurs in allogamous groups without barriers to intrapopulation gene flow. In contrast, more complex, partly sympatric patterns arise in groups with restricted intrapopulation gene flow (Ehrendorfer 1968; Kawano et al. 1971; Kawano 1974). The term “sympatric” differentiation is not used to describe cases involving adjacent populations that are allopatric by geographic criteria; instead, such populations are described as parapatric (Jain and Bradshaw 1966).

The intraspecific differentiation of *C. flexuosa* was compared in Japan and Nepal by assessing morphological, ecological, and genetic characteristics. This comparison is particularly significant, as Japan represents the eastern border of the Sino-Japanese region, while Nepal is near the region's western border.

Six biotypes of *C. flexuosa* growing parapatrically in paddy fields, gardens, and on a stone wall in Japan and Nepal were identified (Kimata and Kobayashi 1996). Seventeen strains were studied. Japanese strains originated from five habitats: a garden, stone wall, roadside, ditch, and fallow paddy field at three locations in Tokyo. Nepalese strains were collected from three habitats: a garden in a mountain area (Syangboche, approximately 4,000 m alt.), two gardens, one in Ratna Park and another at a hotel, and a paddy field (Katmandu, approximately 1,300 m alt.). All specimens were archived at the Herbarium of Tokyo Gakugei University.

Considerable differences in intraspecific crossability among various biotype combinations suggest the presence of intraspecific differentiation among Japanese *C. flexuosa* strains. Such differentiation has been suggested by several morphological and ecological characteristics, including the growing season, seed dispersal mode, germination period, flowering period, among others (Kimata 1983). Notably, the winter annual paddy field biotype forms large populations but is restricted to habitats, such as winter fallow paddy fields. Conversely, the year-long annual garden biotype, which produces fewer seeds, is typically limited to small populations (a few plants per m^2) and prefers wet microenvironments in varied habitats, including gardens, roadsides, and nurseries. F_1 hybrids between the paddy field and garden biotypes in Japan exhibit intermediate traits. At Site 7—a large parapatric habitat for both biotypes—plants exhibit extensive morphological and ecological variation, suggesting ongoing hybridization between these biotypes.

Patterns of phenotypic segregation for six quantitative traits among Japanese F_2 hybrids, along with comparative analysis of ten characteristics between the paddy field and garden biotypes, provide clear evidence for intraspecific differentiation within *C. flexuosa*. For instance, paddy field biotypes are taller than garden biotypes in both Japan and Nepal. However, for six other traits (number of tillers, silique length, width of terminal leaflet, stem color, stem hairiness, and plant form), the variation patterns between Japanese biotypes exhibit opposite trends to those in Nepalese biotypes. This indicates that intraspecific differentiation of *C. flexuosa* in Japan did not occur in parallel with that in Nepal.

Intraspecific differentiation in *C. flexuosa* has proceeded along multiple directions. Crossability studies show that, in Japan, the garden biotype is sexually isolated from the stone wall biotype but not from the paddy field biotype. In Nepal, the garden biotype is sexually isolated from the paddy field biotype due to necrosis in F_1 hybrid seedlings. Similarly, sexual isolation is indicated between the Japanese and Nepalese paddy field biotypes, as hybrid seedlings also exhibit necrosis. Interestingly, the Japanese garden biotype is not sexually isolated from the Nepalese garden biotype, which itself is not isolated from the mountain biotype. Crossing experiments between the Japanese and Nepalese paddy field biotypes further illustrate sexual isolation, although the Japanese paddy field biotype is not strongly isolated from the Nepalese mountain biotype.

Therefore, each garden biotypes in Japan and Nepal represent the prototype among the six biotypes and may be designated as garden "ecotypes." Turesson (1922, 1925) defined an "ecotype" as the product of the genotypic response of ecospecies to a particular, defined set of environmental conditions, while the sub-taxon "ecophene" refers to the reaction type to a unique microenvironment.

Within a limited comparison of Japan and Nepal, a model of intraspecific *C. flexuosa* differentiation was developed. The garden ecotype may represent the original biotype, as neither garden biotype is isolated from the other. Notably, there is no sexual isolation between the garden and paddy field ecotypes in Japan, in contrast to Nepal, where such isolation exists between ecotypes.

Phenotypic variation is observed in the Japanese paddy field ecophene of *C. flexuosa,* consistent with variations found in other weeds inhabiting paddy fields (Sakamoto 1961; Matsumura 1967; Linhart 1974). This diversity in intraspecific differentiation may be linked to the spread of rice cropping throughout Asia. The stone wall ecotype (83011) growing on a stone wall in Koganei, Tokyo, is morphologically, ecologically, and genetically distinct from the garden ecotype (83010). In Nepal, the garden ecotype includes the mountain ecophene. These findings suggest that intraspecific or ecotypic differentiation has occurred independently in Japan and Nepal. Overall, the adaptation of *C. flexuosa* to gardens, paddy fields, and stone walls has followed independent evolutionary paths in Japan and Nepal.

Comparative studies on reproductive systems in *Rorippa cantoniensis, R. islandica, R. dubia, R. indica,* and *R. x brachyceras*, Cruciferae

The genus *Rorippa* was investigated to clarify life cycles and adaptive strategies using ecological genetics and evolutionary biology, with a particular focus on the characteristics of the natural hybrid, *R. x brachyceras* (a perennial, sterile hybrid between the annual *R. islandica* and the perennial *R. indica*). This genus (Cruciferae) comprises approximately 50 species worldwide, five of which are found in Japan. *R. islandica* (Oeder) Boras grows in riversides, wetlands, levees of paddy fields, wheat fields, and orchards in the warm temperate zone from Hokkaido to Kyushu, and similar habitats across Japan, Canada, Australia, and New Zealand. *R. indica* (L.) Hiern is widespread in fields, levees, roadsides, and gardens of Japan, Formosa, China, Korea, Malaysia, and India. *R. cantoniensis* (Lour) Ohwi grows in riversides, wheat fields, and levees from Central Japan to South Korea, China, while Amur. *R. dubia* Hara grows in semi-shaded places from Central Japan to Southeast Asia and South/North America. *R. x brachyceras* has been collected from Japan. Meanwhile, *R. sylvestris* (L) Besser has been collected from sites in Hokkaido and Sugadaira, Nagano in Japan, as well as grows in Finland, Denmark, Switzerland, the Netherlands, Canada, and the United States. *R. austriaca* (Crantz) Besser has been collected from Sakura, Chiba (Victorin 1930, John Wiley & Sons, Inc. 1979).

Among these, *R. cantoniensis* and *R. islandica* are self-pollinated annuals, and *R. dubia* and *R. indica* are self-pollinated perennials. *R. x brachyceras* is considered a hybrid between *R. islandica* and *R. indica* (Kitamura and Murata 1973), while natural and artificial hybrids are sterile perennials. One strain of *R. sylvestris* grown in Nagano is a cross-pollinated perennial, while another grown in Hokkaido is a sterile perennial (Nakatani and Kimata, 1993).

Stebbins (1950, 1957, 1958) observed that annual species tend to be predominantly self-fertilized despite the great diversity of reproductive systems, whereas perennials are generally cross-fertilized, a trend seen in Gramineae, Compositae, and other plant families. This patterns is supported by studies of *Mazus* (Scrophurareaceae) (Kimata, 1978), and *Cardamine* (Cruciferae) (Kimata, 1983; Kimata and Kobayashi, 1996); however exceptions exist—such as the compromised systems found in *Rorippa* (Cruciferae). Self-pollinated annual species are often the most successful colonizers in disturbed habitats due to their ability to produce large quantities of seeds early in the colonization process, aiding in the establishment of new populations (Stebbins, 1958; Ehrendorfer, 1965; Antnovics, 1968; Lefebvre, 1970).

In this context, *R. cantoniensis* and *R. islandica* are excellent annual colonizers, producing numerous small seeds, while self-pollinated perennials *R. dubia* and *R. indica* also succeed via large seed production. These perennials can propagate vegetatively through root and stem segments, particularly following physical disturbance in shady gardens and roadsides. Despite their sterility, *R. x brachyceras* and F_1 hybrids persist through perenniality and vegetative reproduction. Even the annual *R. islandica* demonstrates a considerable capacity for vegetative reproduction if cut during its juvenile stage. Additionally, *R. sylvestris*—whether cross-pollinated or sterile perennial—can colonize effectively via 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* readily hybridize in sympatric populations, such as paddy fields (Figure 9), resulting in the formation of the interspecific hybrid, *R. x brachyceras*. This hybridization is facilitated by the high artificial crossability between the two species, with F_1 hybrids closely resembling *R. x brachyceras* in both morphological and ecogenetic traits. The F_1 hybrid produced by crossing *R. indica* (as the female parent) and *R. islandica* demonstrates vigorous growth, a high seed germination rate, and the ability to persist through perenniality and vegetative reproduction (Kimata and Shibata, unpublished). In contrast, the reciprocal F_1 hybrid (with *R. islandica* as the female parent) exhibits weaker growth and a lower seed germination rate. Both F_1 hybrids are sterile, failing to produce seeds due to pollen sterility, and F_2 hybrids do not grow.

Cytogenetically, *R. islandica* and *R. indica* share the same chromosome number (2n = 16), each with eight bivalents during meiosis. However, their hybrids, including *R. x brachyceras* and their F_1

hybrids possess 16 unpaired chromosomes (monovalents), indicating cytological differences between the parental genomes. *R. islandica* is known to present diploid (2n = 16) and tetraploid (2n = 32) forms due to hybridization events.

Backcrossing the F_1 hybrid (*R. indica* x *R. islandica*) with *R. indica* yields B_1 and B_2 hybrids exhibit robust growth. Although Introgression between *R. islandica* and *R. indica* is theoretically possible, it has not been observed in natural populations. Notably, Japanese interspecific F_1 hybrids do not accept pollen from *R. islandica*, whereas Nepalese interspecific F_1 hybrids accept pollen from both parental species, suggesting that natural introgressive hybridization may occur in Nepal. Furthermore, there are no sexual barriers between Japanese and Nepalese strains of *R. islandica,* while *R. indica* exhibits a sexual barrier.

R. islandica is an annual, while *R. indica* is a strict perennial. The interspecific hybrids, including *R. x brachyceras* and most F1 hybrids, are also perennials. This indicates that perenniality is a dominant trait over annuality. However, two F_1 hybrids derived from Japanese *R. islandica* as the female parent strain tend to show weaker perenniality. Additional research is required to determine whether intraspecific F_1 hybrids between Japanese and Nepalese strains of *R. islandica* display similarly weak perenniality, a trait that may be associated with the potential for vegetative reproduction in juvenile *R. islandica*.

R. indica (2n = 32) features more attractive, larger yellow flowers and produces nectar rich in sugars and amino acids, making it highly appealing to pollinators, promoting outcrossing in this perennial species. In contrast, self-pollinated species like *R. islandica* (2n = 16) do not require such floral adaptations. Observations indicate that *R. indica* receives more frequent visits from pollinators than *R. islandica* and often benefits from secondary visits after pollinators have first visited *R. islandica*. *R. x brachyceras* grows around *R. indica* plants in natural populations. *R. islandica* and *R. indica* cross readily with each other in natural habitats and generate interspecific hybrids. The artificial F_1 hybrid (2X = 24) of *R. indica* x *R. islandica* resembles *R. x brachyceras* (2X = 24) in morphological and ecogenetic characteristics. These hybrids are sterile perennials but show heterosis, grow well, and maintain themselves through vegetative reproduction. Similar hybridization events within the genus *Rorippa* have been recorded in Europe (Howard, 1947; Mulligan and Porsild, 1968). These findings support the conclusion that most *R. x brachyceras* plants are F_1 hybrids originating from crosses between *R. indica* and *R. islandica*.

Analysis of self-pollination rates, calculated from the bagged inflorescences of *R. cantoniensis, R. islandica, R. dubia,* and *R. indica* ranged between 98.1 and 100%. Pollen fertility for these species ranges was 87.4 to 96.2%, while *R. x brachyceras* exhibits a markedly lower fertility rate of 2.5% (Table 8). Open-pollinated flowers of the four species yielded high fructification rates (95.3–100%), whereas that of *R. x brachyceras* was 0%. These data indicate that *R. cantoniensis, R. islandica, R. dubia,* and *R. indica* are self-pollinated, while *R. x brachyceras* is sterile. Petal lengths also vary: approximately 1 mm in *R. cantoniensis* and *R. islandica*, 2.2 mm in *R. x brachyceras,* and 3.5 mm in *R. indica*. *R. dubia* typically lacks petals, although one or two petals may grow irregular cases; usually, these species have four yellow petals.

Regarding reproduction output, the number of siliques per plant is approximately 380 in *R. cantoniensis*, 690 in *R. islandica*, 230 in *R. dubia*, 130 in *R. indica,* and 1,050 in *R. x brachyceras* (Table 8). However, the number of seeds per silique differs: approximately 206 in *R. cantoniensis*, 45.8 in *R. islandica*, 74.0 in *R. dubia*, 79.3 in *R. indica,* and none in *R. x brachyceras*. This equates to highly variable numbers of seeds per plant: ca. 77,900 seeds in one *R. cantoniensis* via many tillers; 30,000 seeds in a *R. islandica*; 16,000 seeds in a *R. dubia*; 9,600 seeds in a *R. indica*, with a few main inflorescences by a few tillers; 77,000 in a *R. cantniensis*; and none in a *R. x brachyceras* plant. Meanwhile, the seed weight of *R. indica* (64.1 mg/1,000 seeds) was similar to that of *R. dubia* (61.5 mg/1,000 seeds), slightly heavier than that of *R. islandica* (50.9 mg/1,000 seeds), and markedly heavier than 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 sprouting roots (b) in Hokkaido

The reproductive systems of *R. 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 many seeds; however, both perennial hybrids are sterile and do not produce seeds. *R. islandica*, *R. dubia*, *R. indica*, and two hybrids have large potentialities of vegetative reproduction by means of root and stem segments. *R. indica* and *R. islandica* can cross to form *R. x brachyceras*, an interspecific hybrid. These reproductive traits may reflect each weedy *Rorippa* species' colonization strategy (Figures 10–12).

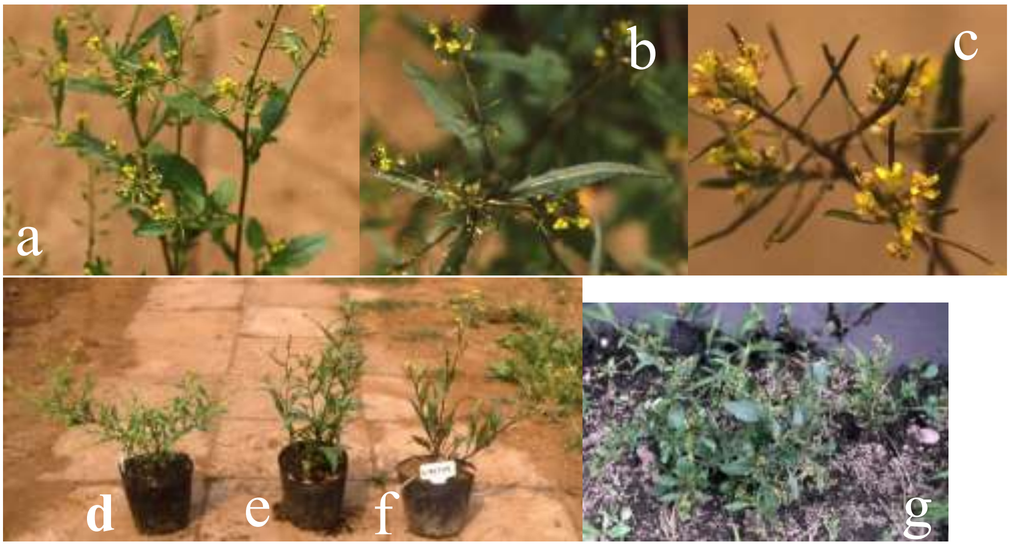


Figure 11. *R. x brachyceras*: an artificial hybrid between *R. islandica* and *R. indica*

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

R. cantoniensis is a winter annual predominantly cultivated in fallow paddy fields, whereas *R. islandica* is a year-long annual species that grows in and near paddy fields but also exhibits aggressive colonization of moist upland fields. *R. dubia* is a perennial commonly found in gardens and along roadsides, while *R. indica* is a perennial species that, in addition to thriving in gardens and roadsides, actively colonizes upland and paddy fields.

R. cantoniensis and *R. dubia* germinate in autumn with subsequent flowering the following spring. In contrast, *R. islandica* and *R. indica* generally germinate twice: first in autumn and again in early summer after fruiting. *R. islandica* primarily flowers during April–May, with infrequent blooming in July–August, while *R. indica* tends to flow from May to June and occasionally from August to September. Co-occurrence of *R. islandica* and *R. indica* in and around paddy fields has also been observed (Table 9). Their overlapping flowering periods in May may facilitate interspecific hybridization, resulting in sterile perennial hybrid *R. x brachyceras*, which reproduces vegetatively.

The reproductive systems of these weedy *Rorippa* species reflect distinct adaptation that support their respective colonization strategies within various 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	rozette	yearlong annual
Cold region		germination, growing, flowering, fructification				summer annual
R. indica	rosette, bolting	flowering, fructification, dormancy		germination, budding	rozette	perennial
R. x brachyceras	rosette, bolting	flowering, sterile	stock dormancy	budding	rozette	perennial
R. cantoniensis	rosette, bolting	flowering, fructification, dormancy		germination	rozette	winter annual
R. sylvestris	rosette, bolting	flowering, fructification, dormancy		germination, budding	rozette	perennial
Hokkaido	rosette, bolting	flowering (sterile)	dormancy, budding from stock and roots		rozett	perennial

The natural habitats of *R. cantoniensis* and *R. islandica* are primarily restricted to fallow paddy fields and levees. Occasionally, *R. islandica* extends its range into upland fields. *R. dubia* thrives in shady gardens, along roadsides, and on levees of upland fields. *R. indica* occupies a broad range of habitats, including levees of paddy and upland fields, gardens, and roadsides. This species often invades paddy and upland fields. *R. x brachyceras* is found in paddy fields and levees. Notably, *R. cantoniensis, R. islandica,* and *R. indica* can grow sympatrically in fallow paddy fields, while *R. dubia* can co-exist with *R. indica* in gardens.

R. cantoniensis is a winter annual, present only from autumn through the following spring. *R. islandica,* in contrast, is an annual that persists throughout the year, although its summer population on the levees of paddy fields in Tokyo remains small. Both *R. dubia* and *R. indica* are observed in all seasons.

Stem segments of *R. cantoniensis, R. islandica, R. dubia, R. indica,* and the F_1 hybrid between *R. indica* and *R. islandica* were prepared at approximately 10 mm in length and 2 mm in diameter, each with one leaf. Roots were similarly segmented at approximately 10 mm in length and 3 mm in diameter. More than 28 segments per species were cultivated on wet paper in Petri dishes maintained at 23 °C and under continuous light of approximately 1,000 lux. After two weeks, the rooting ability from stem segments and sprouting from root segments were assessed.

R. cantoniensis exhibited no rooting from stem segments or sprouting from root segments, indicating it does not produce vegetatively. In contrast, the rooting rate from stem segments was 52.4% for *R. islandica*, 16.0% for *R. dubia*, 8.5% for *R. indica,* and 50.0% for the F_1 hybrid. The stem segments also demonstrated high rates of shoot production, ranging from 54.9% to 91.2% as well as vigorous growth. The sprouting rate from root segments was 78.0% for *R. islandica*, 91.2% for *R. dubia*, 99.4% for R. indica, and 100% for the F_1 hybrid. Shoots derived from root segments grew vigorously and showed rooting rates between 62.0% and 100%.

These data confirm that *R. cantoniensis* lacks the capacity for vegetative reproduction. In contrast, the others possess significant potential for vegetative reproduction through root segments (Table 10). Moreover, *R. islandica* and the F_1 hybrid may propagate via rooting and shooting from stem segments, particularly when cut during weeding in moist fallow paddy fields.

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

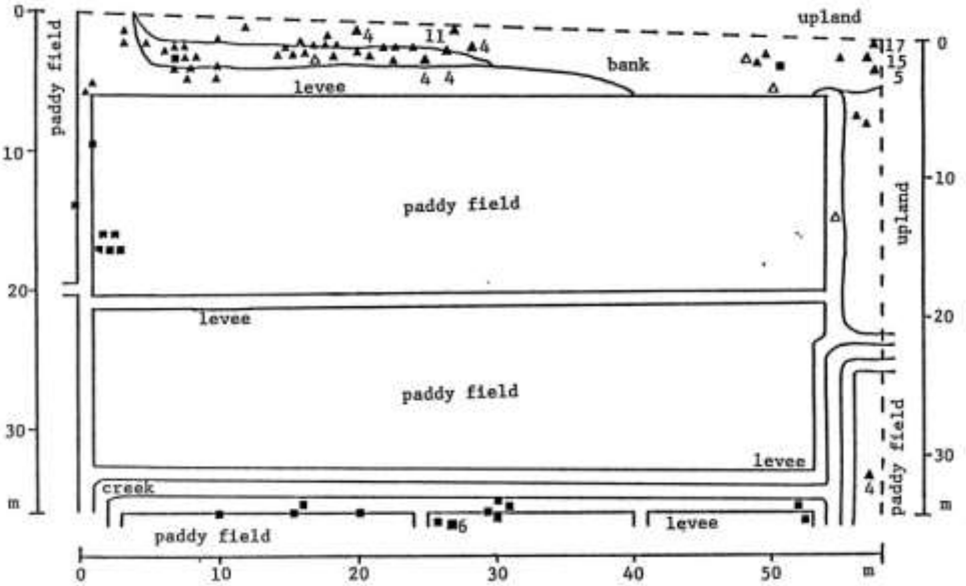
	R. islandica		*R. indica*		Artificial F_1	*R. dubia*	*R. cantoniensis*
No. of root sections	44	106	59	101	113	34	28
No. of sprouts	2.9	2.1	4.1	2.4	3.3	3.9	0
Length of the longest bud (mm)	9.0	5.4	22.7	25.5	30.4	7.7	0
Sprouting rate %	68.2	82.1	100	99.0	100	91.2	0
Greening rate %	61.3	73.6	100	99.0	100	82.4	0
Rooting rate %	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
Length of the longest root (mm)	12.1	4.2	0.5	0.3	2.2	1.8	0
Rooting rate %	76.2	42.9	11.1	7.4	50.0	16	0
Browning rate %	9.5	1.0	0	0	2.1	0	100
Sprouting rate %	92.9	90.5	100	36.1	70.8	86.7	0
Length of the longest shoot (mm)	21.6	11.0	29.2	7.2	17.8	8.1	0

Observation of the hybridization in natural habitats

The five morphological characteristics were compared in *R. islandica*, *R. indica,* and *R. x brachyceras*, their F_1 and B_1 hybrids to identify clearly them in natural habitats. Sympatric populations in rice paddy fields were observed in Kunitachi, Tokyo. *R. islandica*, *R. indica,* and *R. x brachyceras* were observed in and near rice fallow paddy fields (Figure 12). The site A was surrounded by fallow paddy fields on two and a half sides and woody gardens on one and a half sides. The site B was surrounded by fallow paddy fields on three sides and upland field on a side. Both fields were observed on May 28 and Junne 6, 1984. The number of all plants of *Rorippa* species was counted in and around site A practiced winter cultivation already. The number of plants per 1 m^2 was counted at each 1 m mesh divided site B into 274 sections.

The four plants of *R. x brachyceras* were found only in woody garden around site A. The 16 plants of *R. x brachyceras* were dispersed only around the plants of *R. indica* near site B. Great many plants of *R. islandica* and many plants of *R. indica* colonized into site B, where did not cultivate yet at the time observed.

Site A



Site B

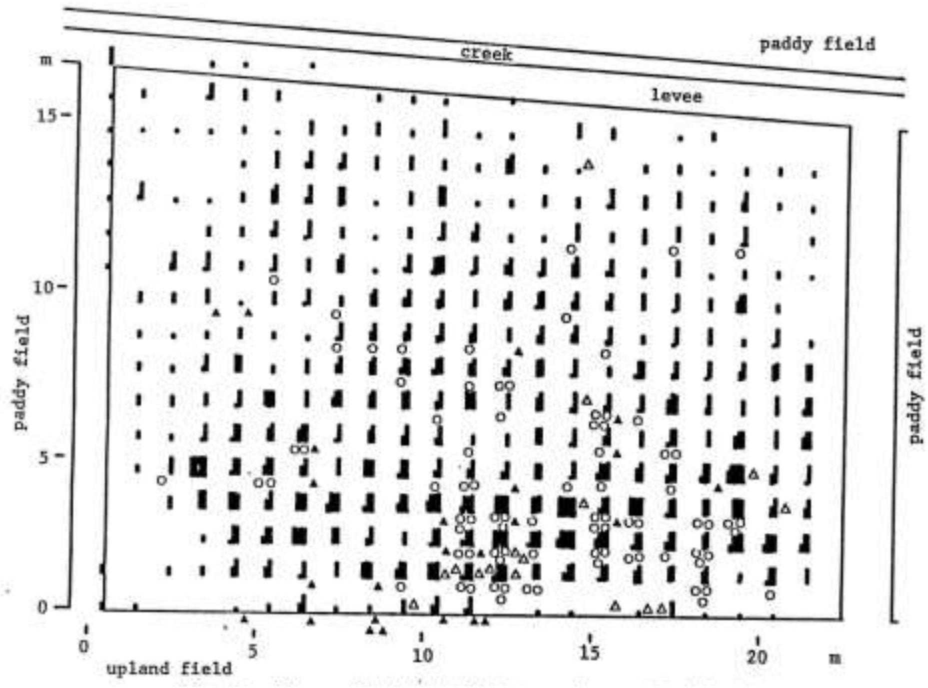


Figure 12. Distribution of *R. islandica*, *R. indica* and their hybrid around rice paddy fields, Site A and Site B.

Site A, Numbers assigned to triangles and quadrats represent the number of plants per m^2; Site B, black bars: number of small silique forms, white circles: large silique forms of *R. islandica;* black triangles: *R. indica,* white triangles: *R. x brachyceras*.

AFLP markers

Murray and Thompson (1980) extracted DNA from 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 using the hexadecyl-trimethyl-ammonium bromide (CTAB) method. The AFLP procedure was performed according to protocols outlined by Applied Biosystems (2005), Bai et al. (1999), and Suyama (2001), with some modifications. Amplification reactions were performed according to the same protocols. Five primers targeting *Eco*RI (E+AAC, E+AAG, E+AGG, E+ACT, and E+ACA) were paired with five 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. The bands, detected using the silver staining protocol described by Cho et al. (1996), were visualized at the highest sensitivity level using Lane Analyzer (ATTO). The raw data were adjusted, and the visible and reproducible bands were scored for accessions as present (1) or absent (0).

The AFLP marker dendrogram was constructed using neighbor-joining and UPGMA methods (Nei and Kumar 2000) with bootstrap analysis (PAUP* ver. 4.0) and hierarchical cluster analysis (group average method, SPSS ver. 21) for all samples matrices (Figure 13). The resulting AFLP dendrogram provides a clear phylogenetic tree, confirming that *R. x brachyceras* is a natural hybrid between *R. islandica* and *R. indica*.

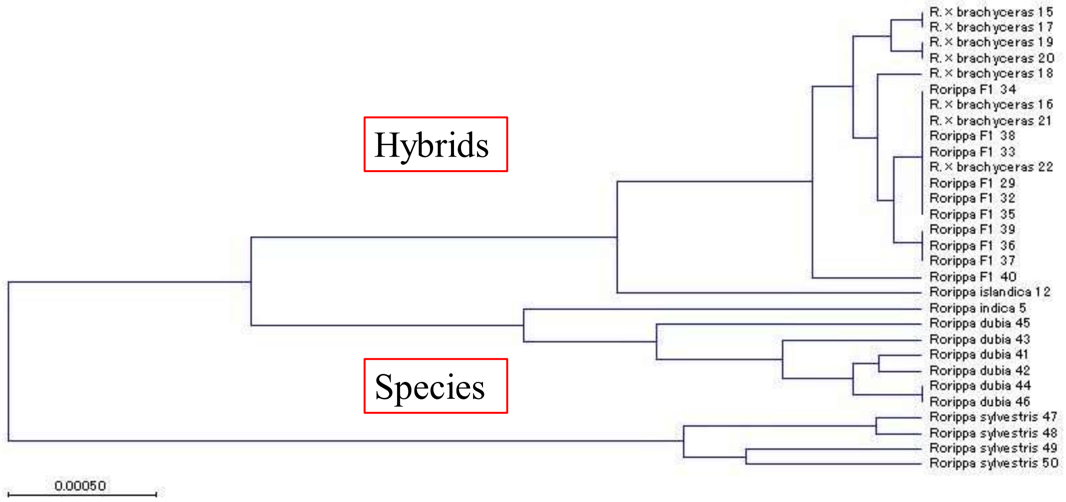


Figure 13. AFLP dendrogram of *Rorippa* by UPGMA

Chapter 3 Evolution of the Poaceae

The grass family, Poaceae, though not the largest in terms of species or genera—being surpassed by families such as Compositae—holds immense importance due to its global impact. Grasses provide the extensive grasslands that cover approximately one-third of the Earth's surface and include cereal crops that form the staple food for much of the world's population. The evolutionary success of grasses is reflected in three recurring themes: their high adaptability to variable environments; their ability to coexist with grazing herbivores and humans; and their possession of a distinctive lifeform suited to a seasonal life cycle. Typically, perennial grasses dominate during adverse seasons, while annuals overwinter as seeds, a strategy generally regarded as highly advanced due to its high reproductive efficiency (Clayton and Renvoize 1986).

Chapman (1996) provided an excellent overview of Poaceae. Both Poaceae (rice order) and Cyperaceae had differentiated from Commelinales. The Poaceae family comprises approximately 10,000 spices. Grasses began evolving their distinctive features long before the emergence of *Homo sapiens*. Adaptations such as linear leaves and small green flowers, which confer drought tolerance, have enabled grasses to thrive in open habitats and often establish themselves as pioneer species or early colonists. Perennial grasses are well adapted for vegetative reproduction. The evolution of annual or ephemeral forms from perennial ancestors is a notable trend, with the shift being particularly interesting in grasses.

Many annual grasses, including wheat and barley, retain the ability to produce tillers. These tillers, with adventitious roots, can be separated from the mother plant and propagated independently. The transition to an annual growth habit involves a massive commitment to seed production, sufficient to cause senescence of the plant. This process is irreversible, although the introduction of genes from *Agropyron* into wheat can induce a perennial habit. The emergence of C_4 photosynthesis is thought to be in response to low atmospheric CO_2 levels during the Tertiary period. The advent of agriculture led not only to the selection and cultivation of preferred plant species but also to the incidental propagation of weeds, which survive independently and can impede agricultural productivity.

Poaceae are anemophilous, i.e., adapted for wind pollination, and have thrived in diverse environments across the world (Hotta 1974, Tamura 1974). Wind pollinated plants produce numerous pollens, promote cross-pollination and then expand genetic diversity.

Growth Habits and Patterns of C*oix lacryma-jobi* var. *ma-yuen* and var. *lacryma-jobi*, Poaceae

The ecogenetic differences in growth habits and patterns were compared between the cultivated annual variety, C*oix lacryma-jobi* var. *ma-yuen* (Sakamoto et al., 1980), and its closely related wild perennial counterpart, C*oix lacryma-jobi* var. *lacryma-jobi.* Taxonomists have classified var. *ma-yuen* as a domesticated annual species (Makino 1948; Ohwi 1953), while var. *lacryma-jobi* is recognized as a wild perennial. Comparative analysis of these two varieties provided experimental evidence concerning intraspecific differentiation from perennial to ecologically annual forms.

Two varieties—C*oix lacryma-jobi* L. var. *ma-yuen* and var. *lacryma-jobi*—along with two F_1 and one F_2 hybrid strains were evaluated. The wild variety C. *lacryma-jobi* L. var. *lacryma-jobi* (strain no. 76501) was collected from Kamakura-shi, Kanagawa Prefecture, in 1975, while the domesticated variety C. *lacryma-jobi* var. *ma-yuen* (Roman.) Stapf (strain no. 76505) was obtained from the Agricultural Station of Toyama Prefecture in 1975. Reciprocal crosses between these varieties in 1975 (crossability ca. 60–70%) resulted in 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 to avoid pollination by alien pollen (Kimata and Nakagome 1982; Sakamoto, Kimata and Kawase 1980).

Floristic studies have described C. *lacryma-jobi* L. var. *lacryma-jobi* as perennial and var. *ma-yuen* as annual (e.g., Makino 1948; Ohwi 1953). In controlled growth cabinets, all C. *lacryma-jobi* L. var. *lacryma-jobi* plants and 22.2–88.9% of var. *ma-yuen* survived. In upland field plots, the survival rate of var. *lacryma-jobi* was 80% in 1976 and 16.7% in 1977, while no var. *ma-yuen* plants survived in 1976 or 1977. Among the F_1 strains, no 76506 plants survived, while16.7% of 76508-1 did. Both varieties died under extreme low (under frost) or high (under dryness) temperatures. Murakami and Harada (1958) reported that 20% of var. *ma-yuen* and all var. *lacryma-jobi* and their F_1 strains survived the subsequent growing season in upland fields of Kyoto. The F_2 survival rate was approximately 80% (Murakami 1961) in Kyoto and 61% in Tokyo. Moreover, two var. *ma-yuen* strains collected from North Halmahera, Indonesia in 1976 were maintained vegetatively in an unheated greenhouse for at least three years (Sakamoto et al., 1980). These observations support the conclusion that *C. lacryma-jobi* var. *lacryma-jobi* is perennial, while var. *ma-yuen* is potentially perennial but ecologically annual, exhibiting weak cold resistance.

The seeds of var. *ma-yuen* germinated more rapidly than those of var. *lacryma-jobi*. F_1 hybrids exhibited intermediate germination patterns between the two parents, while F_2 progeny demonstrated the same pattern as var. *ma-yuen* (Fig. 14). Rapid germination in var. *ma-yuen* is characteristic of annual plants. The rate of increase in plants height and tiller number was higher in var. *ma-yuen,* reaching a plateau sooner than var. *lacryma-jobi*. This indicates an annual growth pattern in var. *ma-yuen* and a perennial pattern in var. *lacryma-jobi*. F_1 hybrids exhibited intermediate growth, and F_2 progeny showed a bimodal distribution in plant height, with one peak corresponding to var. *ma-yuen* parent and the other showing transgressive segregation (Murakami, 1961). The distribution of tiller number in F_2 followed a normal curve, with most F_2 plants demonstrating vigorous growth but limited tillering capacity.

The heading date of var. *ma-yuen* was earlier than that of var. *lacryima-jobi*, a trait typical of annuals, while the later maturation of var. *lacryima-jobi* is consistent with perennial behavior. F_1 hybrids had intermediate heading dates, while F_2 progeny exhibited a bimodal distribution: the earlier group matched that of var. *ma-yuen,* while the latter group corresponded to var. *lacryma-jobi*. Murakami (1961) suggested a trihybrid segregation ratio for heading date in F_2 (segregation ratio 10:54 = early var. *ma-yuen* type: late var. *lacryma-jobi* type). However, the observed segregation ratio (4:5) did not agree with this assumption. Moreover, the heading date of the two parents was later, with less distinction between parental heading dates than in Murakami's study, indicating the need for further examination.

The pollen fertility is higher and the protogyny is lower in var. *ma-yuen* than var. *lacryma-jobi*, resulting in greater grain fertility of var. *ma-yuen*, although the grains are lighter. Murakami et al. (1960) reported weak sexual isolation between these varieties, which was also observed in F_1 hybrids in the current study.

The allocation of dry matter to reproductive structures in var. *lacryma-jobi* reaches ca. 11% (9.1g) of the total plant dry weight, while var. *ma-yuen* allocates 20% to grains at the end of the growing period. Kawano and Hayashi (1977) reported up to 41% reproductive allocation in var. *ma-yuen*. In contrast, the subterranean stems accounted for 6% (5.0g) in var. *lacryma-jobi* and 2% (0.9g) in var. *ma-yuen* at the end of the growing period. Var. *lacryma-jobi* directs more energy to vegetative growth and less to sexual reproduction than var. *ma-yuen*. These reproductive traits indicate that var. *ma-yuen* is annual, while var. *lacryma-jobi* is perennial (cf. Kawano 1975).

McNaughton (1975) reported that *Typha* populations in short growing seasons produce numerous small rhizomes due to high winter mortality. Similarly, *C. lacryma-jobi* var. *lacryma-jobi* produces more tillers with dormant buds and ratoons from cut stumps than var. *ma-yuen*. However, correlations do not exist between the total tiller number and winter survival rate, though a weak positive relationship exists between non-productive tillers and winter sprouting. Thus, tillering capacity is not closely linked to wintering habit in *Coix*, and further physiological and genetical research is needed to clarify these mechanisms.

Oka and Morishima (1967) noted that perennial strains of *Oryza* root more easily from culm segments than annual strains, linking vegetative reproduction to perenniality. Two *C. lacryma-jobi* varieties exhibit high rates of rooting and sprouting from culm segments, with no significant differences between them. This suggests that var. *ma-yuen,* despite its ecological annualism, retains the potential for perennial growth.

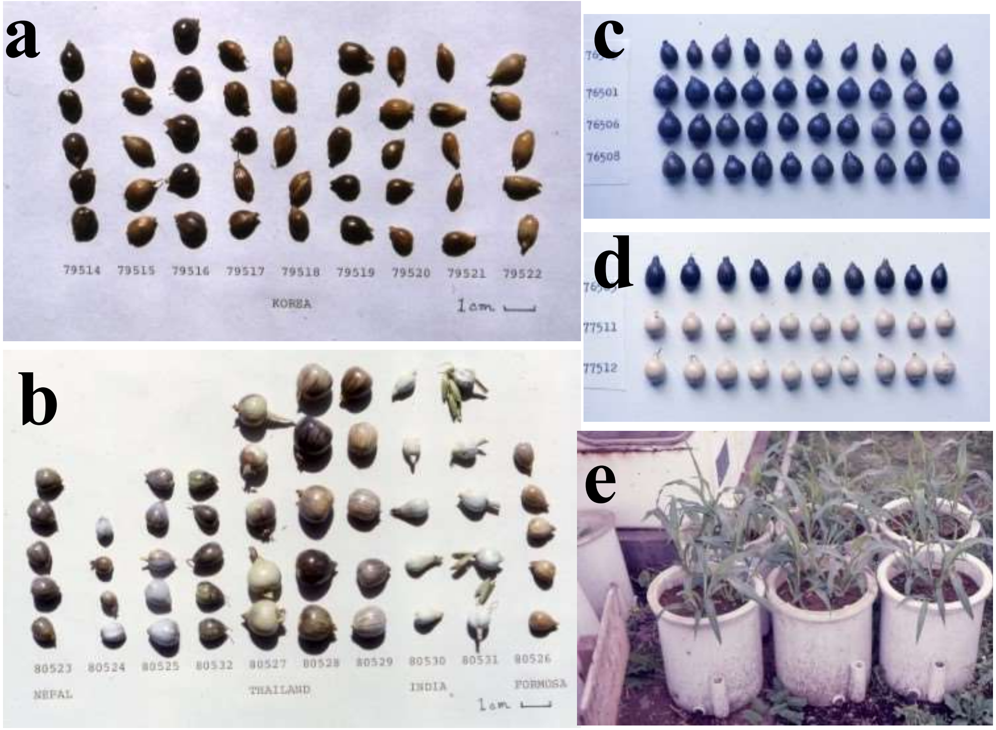


Figure 14. Morphological variation of bract sheaths in *Coix lacryma-jobi*
a–d, bract sheath; e, var. *ma-yuen* (upper) and var. *lacryma-jobi* (lower)

Based on comparative studies of growth patterns, reproductive systems, and tillering capacity, it can be concluded that *C. lacryma-jobi* var. *ma-yuen* functions ecologically as an annual but possesses latent perennial capabilities. In contrast, var. *lacryma-jobi* is clearly perennial (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 habits of genus *Zea*

Zea mays (maize, annual), teosinte (Figure 15), and *Tripsacum* are the three key New World members of the tribe Maydeae. Teosinte (2n = 20) is a weedy annual closely related to maize (2n = 20). Although maize and teosinte are morphologically similar, they differ notably in female inflorescence structures and chromosome knob patterns, enabling fruit case dissemination (Figure 15). Maize differs in that it lacks natural seed dispersal and seed dormancy, making it wholly dependent on human cultivation for propagation (Goodman 1995).

Oriental Maydeae, including *Coix,* are generally considered to be distantly related to maize (Mangelsdorf 1974). However, speculation exists that *Coix*—with knobbed chromosomes in multiples of x = 5—may be more closely related to maize than other oriental genera.

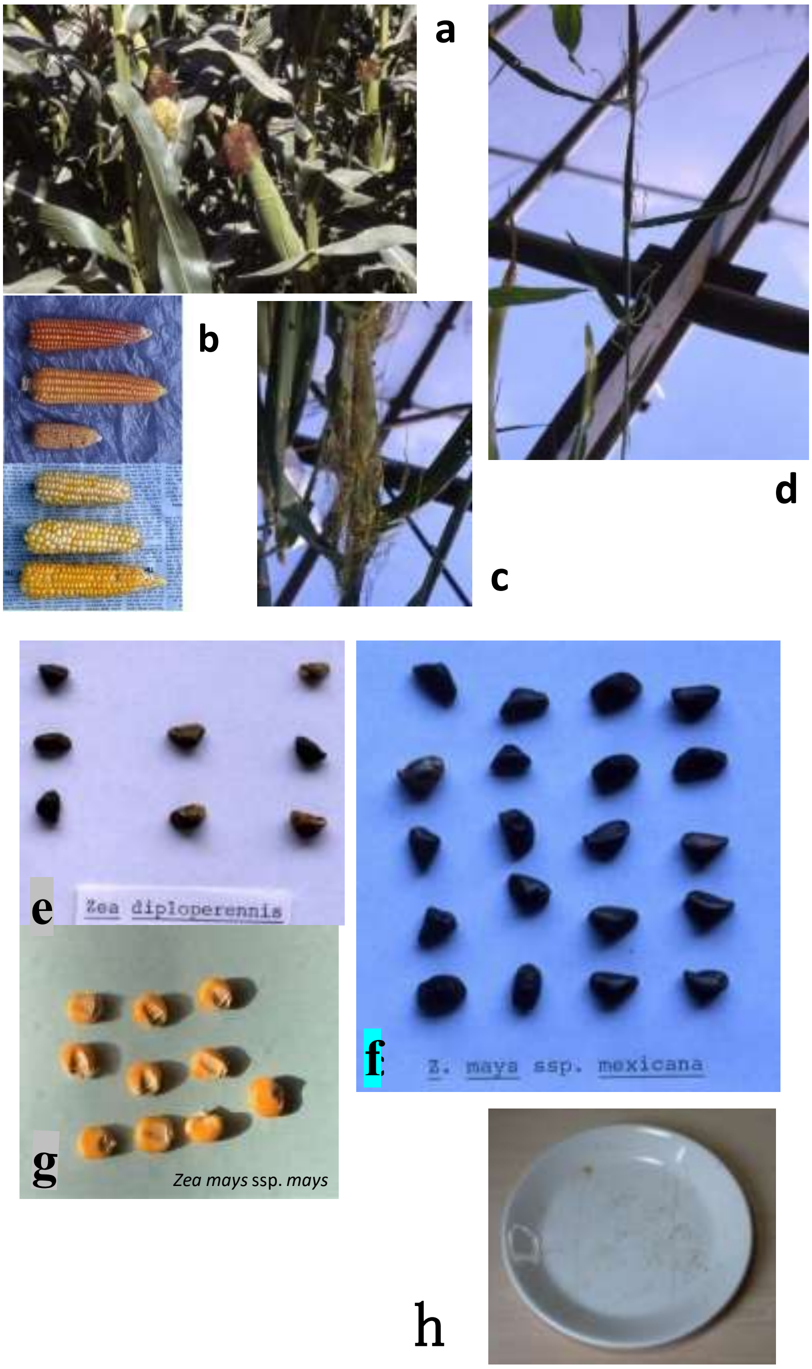


Figure 15. Ears and seeds of genus *Zea*

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; h, *Z. diploperennis* illustrated by Iltis (1983).

Guzman discovered a substantial population of grass and sent seeds to Iltis (1983, 1987; Fussell 1992). Upon cultivation, Iltis determined that the plants had the same number of chromosomes as maize, leading to the identification of a new species: *Zea diploperennis*, or perennial teosinte.

I had learned about maize evolution directly from Iltis during the US–Japan Science Seminar at the New York Botanical Garden in 1983, after which he sent me *Z. diploperennis* seeds for analysis

(Figure 15d, e).

Differentiation of ecotype in genus *Agropyron* (Poaceae)

The early ecotype (ecological annual) of *Agropyron tsukushiense* (Honda) Ohwi var. *transiens* (Hack.), which is adapted to fallow paddy fields, is ecologically and genetically distinct from the common type that inhabits roadsides, levees, and other disturbed habitats (Sakamoto 1961). A closely related species, *A. humidorum* Ohwi et Sakamoto, grows in fallow rice paddy fields, often sympatrically with the early ecotype of *A. tsukushiense* var. *transiens* (Ohwi and Sakamoto 1964; Sakamoto 1978). Therefore, the relationship between growth habit and habitat for those two species was investigated.

Field observations

Four winter fallow paddy fields, designated Plot-1, Plot-2, Plot-3 and Plot-4, in the suburbs of Mishima-shi, Shizuoka Prefecture, were studied. In Plot-1, a mixed swarm of the early ecotype of *A. tsukushiense* var. *transiens* and *A. humidorum* were found. In Plot-2, the former was abundant and the latter was rare, while the opposite pattern was detected in Plot-3. Plot-4 was dominated by *A. humidorum,* with few early ecotype individuals. Seedlings from seeds and propagules produced from culm segment were counted using the 1-m^2 quadrat method in Plot-1 on November 21, 1975 and November 22, 1976. Soil surface samples (10 cm) were collected to measure the depth at which seedlings and sprouting propagules were found.

Further sampling in Plot-2 and Plot-3 on January 16, 1978, involved counting germinating seeds and sprouting or non-sprouting segments in 3–5 randomly selected soil clods (50 cm length × 50 cm width × 10 cm depth = 0.025 m^3). The relationship between the number of culm segment nodes and their sprouting rate in *A. humidorum* was also examined in Plot-4.

Seed germination and sprouting of culm segments under various conditions

Three strains from Mishima-shi, Shizuoka Prefecture, were observed. Seeds were stored under upland, lowland and dry conditions, with five temperature regimens: 1) daytime 35 °C/nighttime 25 °C; 2) daytime 25 °C/nighttime 15 °C; 3) constant 20 °C; 4) constant 6 °C; and 5) natural temperature conditions in 1976. This resulted in 14 experimental water and temperature plots. Upland seeds were packed in nylon-net bags and stored in loam soil watered every several days; lowland seeds were submerged in loam soil; dry seeds were stored in sealed cans with silica gel. Every 15 days, seeds were removed and evaluated for germination using unglazed germination plates under continuous light (8,000 lux) and 25 °C.

Culm segments with one node were stored under upland and lowland conditions and exposed to four temperature regimens: 1) daytime 35 °C/nighttime 25 °C; 2) daytime 25 °C/nighttime 15 °C; 3) constant 20 °C; 4) natural temperature conditions in 1975 and 1976. Thus, eight experimental plots were created. Every 15 days, 30 stored culm segments were removed from each plot and assessed for sprouting on wet filter paper in Petri dishes under continuous light (8,000 lux) and 25 °C.

According to Sakamoto (1978), the natural life cycle of the early ecotype of *A. tsukushiense* and *A. humidrum* reflects the traits of typical winter weeds in fallow paddy fields. Near the point of maturation for two species, rice cultivation begins, dispersing seeds and culms throughout the soil.

During summer rice cultivation, these propagules remain dormant. By mid-September, seeds and propagules begin to germinate and sprout, while young plants reach the tillering stage during rice harvest in October–November. Thus, these species are temporally separated from rice plants yet often grow sympatrically, having adapted successfully to winter fallow paddy fields.

Moreover, a remarkable difference in reproduction mode was detected between these two species. In natural habitats, the clone of the early ecotype typically dies within a year and reproduces exclusively by seed, behaving ecologically as an annual plant despite being perennial under upland conditions. Therefore, this ecotype is defined as an ecologically annual but potentially perennial. In contrast, *A. humidorum* reproduces both sexually by seeds and asexually via propagules from culms.

Compared to the common type, the early ecotype and *A. humidorum* demonstrate clear adaptation to paddy fields. Their seeds maintain germination ability under natural lowland temperatures. According to Ohwi and Sakamoto (1964), adaptation to moist environments is particularly pronounced in *A. humidorum*, as evidenced by two traits: the formation of an abscission layer at maturity below the flag leaf node, allowing spikes to detach easily; and the perennialization of culms with the exception of the uppermost internode and spike, from which new shoots and roots readily develop when conditions are favorable.

Experimental results further revealed that dormancy of seeds and culm segments from June to September under lowland conditions is an additional adaptive feature of *A. humidorum* (Figure 16). Overall, these observations indicate that *A. humidorum* is more strongly adapted for vegetative propagation through perennialized culms or clones than for sexual reproduction by seeds.

Notably, two closely related species can develop distinct strategies in winter fallow paddy fields, despite adapting to similar environmental conditions.

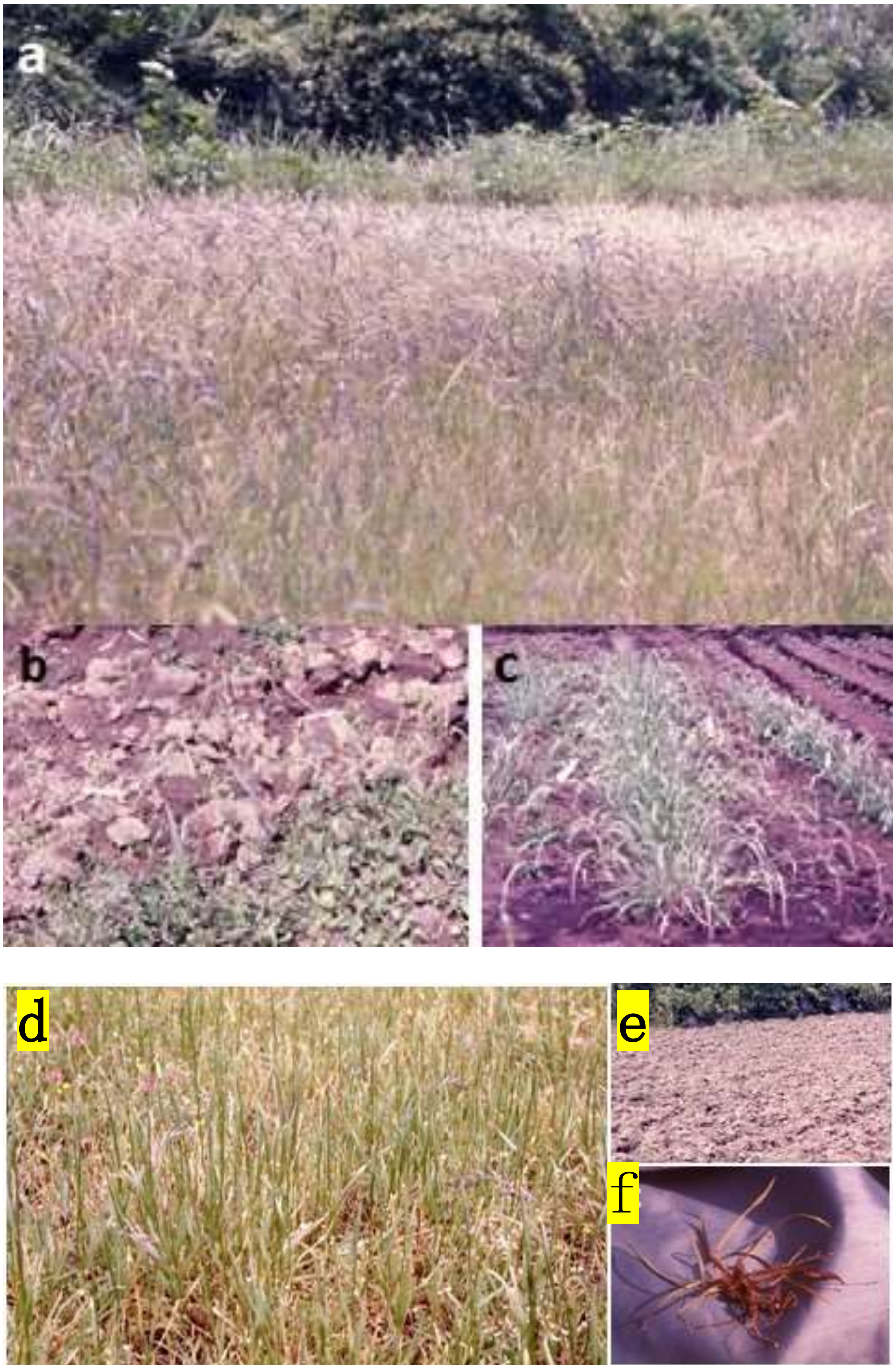


Figure 16. Weeds of genus *Agropyron*

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 Tokyo Gakugei University field; d, a sympatric population of early ecotype and *A. humidorum*; e, after spring plowing in the same sympatric population; f, sprouting from culm sections in soil of a fallow field after spring plowing.

Life history of genus *Secale*, tribe Triticeae

Rye is the most cold-tolerant cereal in temperate regions and can be sown in winter and spring, though spring yields are lower. The annual weedy group of *Secale* evolved from perennial *Secale* *montanum* in the Far East (Figure 17). Through domestication, this annual weed lost seed shattering, developed erect growth, and larger grains, leading to the cultivation of *Secale cereale* (outcrossing annual). Meanwhile, *Secale montanum* diversified into *S. silvestre* and *S. vavilovii* (self-pollinated annual), with adaptation involving chromosomal rearrangement and a shift from perennial to annual life cycles.

Archaeological evidence shows rye was domesticated ca. 3,000–4,000 BC. By AD 20, a third of Europeans ate rye bread before gradually shifting to wheat bread (Stebbins 1950, 1957, 1958; Riley 1955, Khush and Stebbins 1961, Khush 1963, Suneson et al. 1969, Evans 1996).

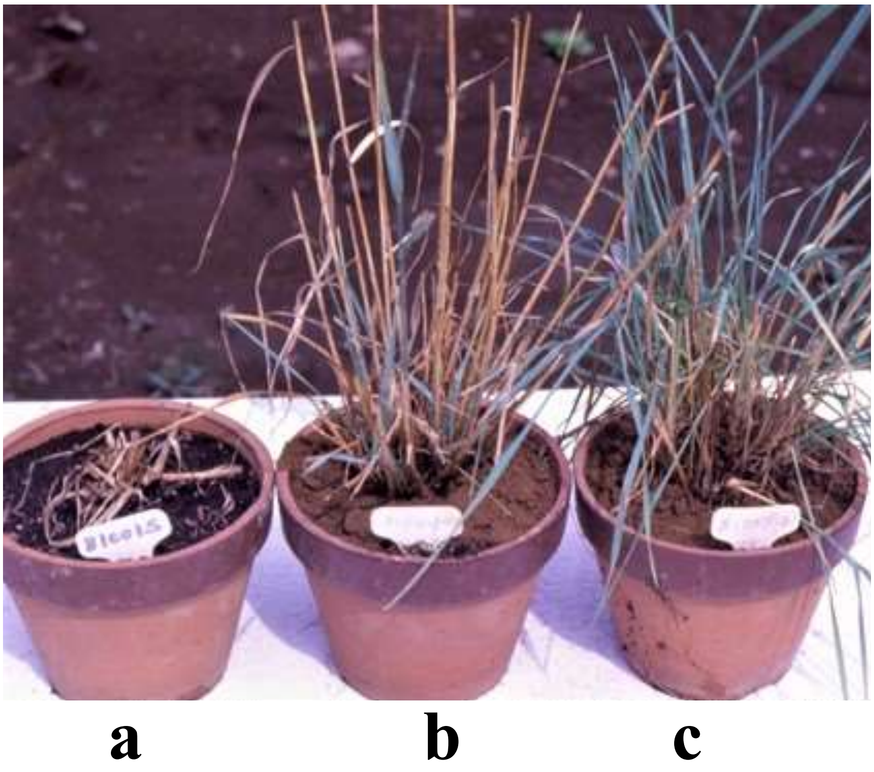


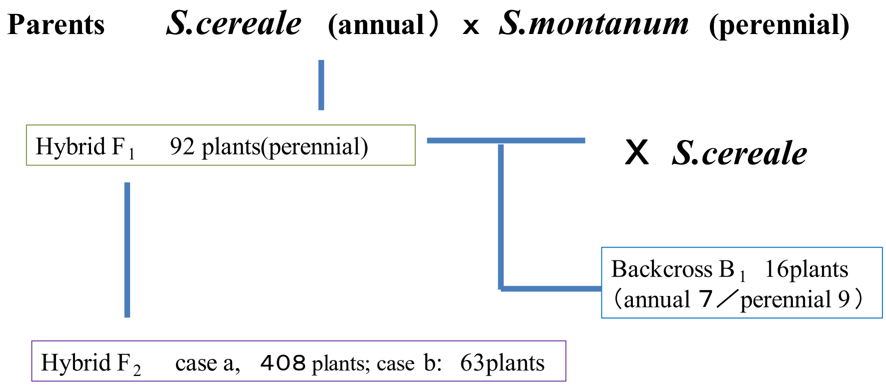
Figure 17. Hybrid F_1 (c, perennial) between *Secale cereale* (a, annual) and *S. montanum* (b, perennial)

The wild form of *S. cereale* is distributed widely from Central Europe to the Balkan Peninsula, Anatolia, Israel, Trans-Caucasia, Iran, Central Asia; Afghanistan, with a small isolated population also found in South Africa. All *Secale* species are diploid (2n = 14). These species commonly invade disturbed habitats by natural processes and human activities, and are particularly prevalent as weeds in wheat and barley fields.

Secale cereale began as a secondary crop that was domesticated from companion weedy rye. As wheat and barley cultivation spread northward and to highlight regions, these crops faced colder and more barren conditions. When severe cold weather struck, wheat and barley yields often suffered, whereas rye yields remained relatively stable. This resilience to cold led to the domestication of *S. cereale* from its weedy ancestor, as it demonstrated strong tolerance against cold conditions (Vavilov 1926). The domestication of rye is a continuous process, still progressing in agricultural fields (Sakamoto and Kawahara 1979).

The domestication of rye is particularly notable when compared to the process for Indian millets. The primary limiting factor in rye domestication was cold tolerance, while drought tolerance was key in the domestication of Indian millets. Rye was domesticated from companion weeds found among wheat and barley crops, whereas Indian millets originated from companion mimic weeds in rice fields. For millets, drought tolerance was critical for cultivation in the Decan Plateau (Kimata 2016).

Artificial hybridization between *S. cereale* (annual) and *S. montanum* (perennial) resulted in an F1 hybrid that exhibited a perennial growth habit (Figure 18). The perennial habit was dominant, but segregation in the F2 generation was complex, with some plants failing to head or experiencing necrosis. The inheritance of growth habits is not determined by a single 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*

Growth habit in *Secale* is influenced by various morphological, ecological, and genetic characteristics. Annual growth is clearly dominant over perennial. The number of nonproductive tillers is closely related to maintaining dormant buds for polycarpic growth. *S. cereale,* as an annual, does not retain nonproductive tillers, such as late-emerging heads and foliage buds, by the end of July. In contrast, *S. montanum* typically has 21–30 nonproductive tillers, while the F1 hybrid can have 51–60, forming tussocks. Annual F2 hybrids lack nonproductive tillers, but perennials are highly variable, with tiller numbers ranging from 1 to 90. Artificial selection during domestication has focused on reducing nonproductive tillers.

Domestication process of wheat

Many important cereals and fodder crops belong to the sub-family, Festucoideae (family, Poaceae). In the tribe Triticeae (Table 11), the genus *Agropyron* consists exclusively of perennials, while *Secale* and *Hordeum* include both annual and perennial species. In contrast, *Triticum* and *Aegilops* comprise only annuals (Satake 1964, Sakamoto 1991, 1996; Kihara ed. 1954; Clayton and Renvoize 1986).

The fifteen genera of Triticeae are divided into two major groups based on geographical distribution: the Mediterranean group and the Arctic-temperature group (Sakamoto 1973). The former is predominantly made up of self-fertilized annual species, while the latter primarily consists of perennials, both self- and cross-fertilized. Rapid adaptive differentiation occurred in the Mediterranean group during the formation of the Mediterranean climate, likely in the Quaternary, which is characterized by hot, dry summers and cool, moist winters. Annual species adapted to overwintering conditions, with most winter annuals originating from Mediterranean-Central Asiatic regions.

Comparisons among the 15 genera of Triticeae reveal that most annual species are distributed from the Mediterranean to Central Asia, whereas perennial species are found in circumarctic and temperate zones. The dry summer climate of the Mediterranean to Central Asia was a center of domestication for wheat, barley and other crops, fostering the development of ancient agricultural cultures approximately 12,000 BP. Winter annuals germinate in autumn, overwinter, bloom, and subsequently bear fruit (Sakamoto 1973).

Triticeae underwent rapid adaptive radiation and morphological diversification, particularly during periods of topographical change caused by the Alpine orogeny. This led to close genetic relationships and frequent hybridization among species and genera, resulting in the differentiation of both allopolyploid and autopolyploid forms.

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)

Annual plants complete their life cycles and die within 12 months, although this period can span two calendar years if the plant overwinters. There are two categories of annual life cycles: one ends fairly abruptly after flowering and seed production (these are considered "true" annuals), while the other has a potentially indefinite lifespan that is typically terminated within one year by climatic events—these plants are known as ecological annuals or potential perennials (Harper 1977). Many Mediterranean grasses and plants found on cultivated land fall into the first category, where annuals are relatively safe until harvest and make use of their growth period without interruption. However, the adaptive value of the second category remains largely unexplored.

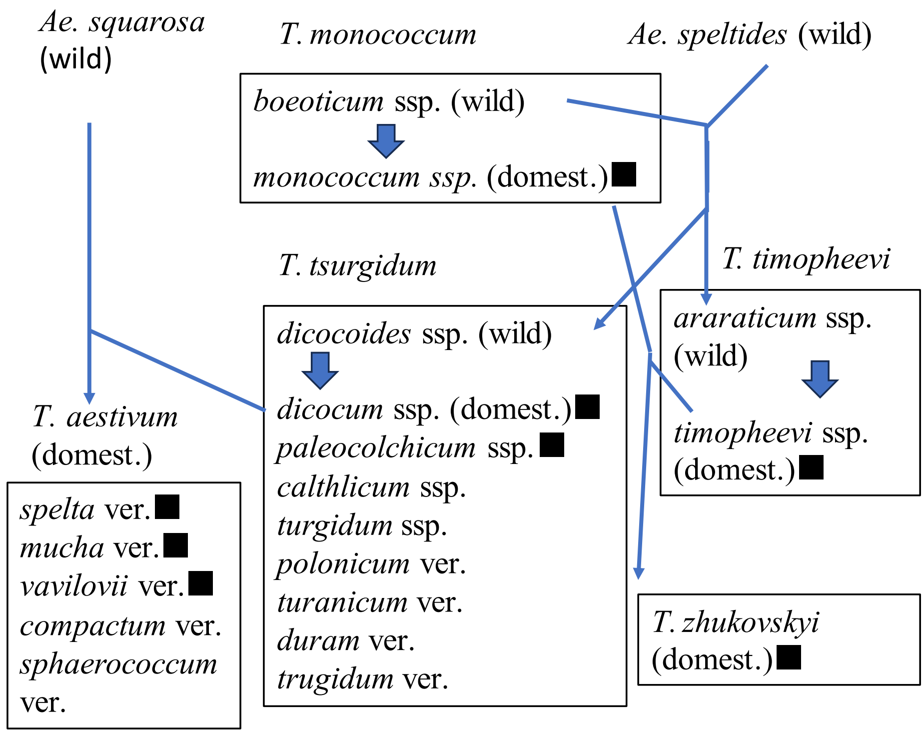


Figure 19. Origins and domestication of five groups in genus *Triticum*

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

(modified Sakamoto 1985,1996; Ohta original)

The domestication process of wheat was intricate, primarily involving annual species, with multiple species contributing to the overall trajectory (Figure 19). Sakamoto (1996) classified wheat into five distinct groups (Table 12). Among these, wild and domesticated subspecies exist for *T. monococcum*, *T. turgidum* and *T. timopheevi*. Specifically, each of these wheat types was domesticated from its respective wild subspecies: *T. monococcum* ssp. *boeoticum*, *T. turgidum* ssp. *dicoccoides* and *T. timopheevi* ssp. *araraticum*. In contrast, no wild species are associated with *T. aestivum*.

Research indicates that *T. aestivum* was domesticated as a hybrid between *T. turgidum* and *Ae. squarrosa*. *T. aestivum* is amphidiploid and considered a secondary crop, having involved a companion weed in its domestication pathway. The distribution of *Ae. squarrosa* ranges from Trans-Caucasus, Eastern Turkey, Iran, Afghanistan, and Central Asia to Western China. In Iran, *Ae. squarrosa* is recognized as a weed in wheat fields. *T. aestivum* incorporated the D genome from a subspecies native to the east cost of the Caspian Sea and the Trans-Caucasus, and domestication occurred in this region.

Ehrendorfer (1965), Ornduff (1969), and Stebbins (1974) highlighted the relationship between self-fertilized annuals and higher polyploidy, which helps avoid the disadvantages of a homozygous genotype (Table 11). These species are typically cross-fertilized by wind pollination, though high self-pollination rates are also observed. However, within the tribe Triticeae, many polyploid species do not have a direct relationship to their growth habit.

An expedition to Central Asia in 1993 resulted in the collection of numerous Triticeae species (Table 12 and Figure 20). The number of collected accessions included 47 from *Triticum*, 37 from *Hordeum*, 26 from *Aegilops*, and 17 from *Agropyron*. Natural hybridization among these species continues in wheat fields. Species identification was carried out by the Plant Germ-Plasm Institute at Kyoto University, and field experiments in 1994. For comparative purposes, *H. bulbosum* (2n = 14, 28), a perennial species, with rhizomes and polycarpy, was cultivated alongside these accessions.

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 depicts an ancient wheat field contaminated with various weedy species, such as poppy, corn cockle, rye, and oat. Barley (*Hordeum vulgare*) is a self-pollinating diploid (2n = 2x = 14). While tetraploid forms have arisen spontaneously, they represent only a negligible portion of cultivated barley. Wild and weed races, generally designated *H. spontaneum*, biologically belong to the same species as domesticated varieties (Harlan 1995).

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

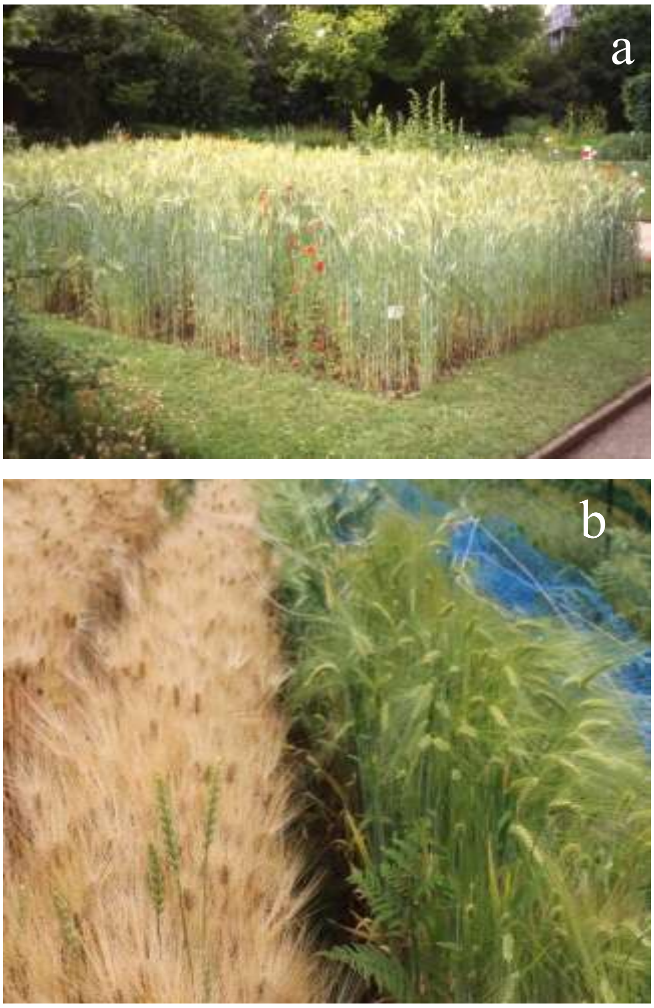


Figure 21. Wheat and barley

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

Growth habits of *Sorghum*

Sorghum is a highly diverse genus (de Wet 1978, Heran 1979, Sakamoto 1988). *Sorghum bicolor* (L) Moench is an annual diploid plant (2n = 20; Figure 22) derived from *S. bicolor* var. *verticilliflorum* in Eastern Africa. *S. halepense* (L) Pers. is a tetraploid perennial weed (2n = 40) with two subspecies: A Mediterranean ecotype, small with slender leaves, distributed from Asia Minor to the western mountainous region in Pakistan; and a tropical ecotype, larger with wide leaves (2n = 20), distributed from South India to Southeast Asian islands.

S. propinquum (Kunth) Hitchcock is a perennial diploid (2n = 20) distributed from Sri Lanka to South India, Myanmar and Southeast Asian islands. In the Philippines, hybrids between this species and *S. bicolor* are perennial and considered serious weeds. Hybrids among *S. bicolor*, *S. halepense,* and *S. propinquum* are perennial triploids or tetraploids that propagate vigorously via rhizomes. This illustrates that perennial growth habit is a dominant trait. Breeding efforts focus on traits that prevent soil degradation and improve fodder crop qualities (Quinby *et al.* 1958, Cox *et al*. 2018).

In Central Asia, 52 sorghum accessions were collected and classified into five types according to panicle form. The broom type (15 accessions) was widely cultivated in kitchen gardens throughout West Turkestan and was prized for making long brooms due to its long sparse panicles (-70 cm). The weedy type (3 accessions) featured sparse panicles with many tillers. The sugar A type (7 accessions) had conical panicles and exhibited significant variation, while the sugar B type (14 accessions) had spear-like panicles and fewer tillers. These sugar types served as genetic resources for sugar production at Leningrad University. The grain type (10 accessions) had drooping ovate-compact panicles and few tillers. Despite the remarkable diversity of *S. bicolor* in this region, perennial weedy types were absent.

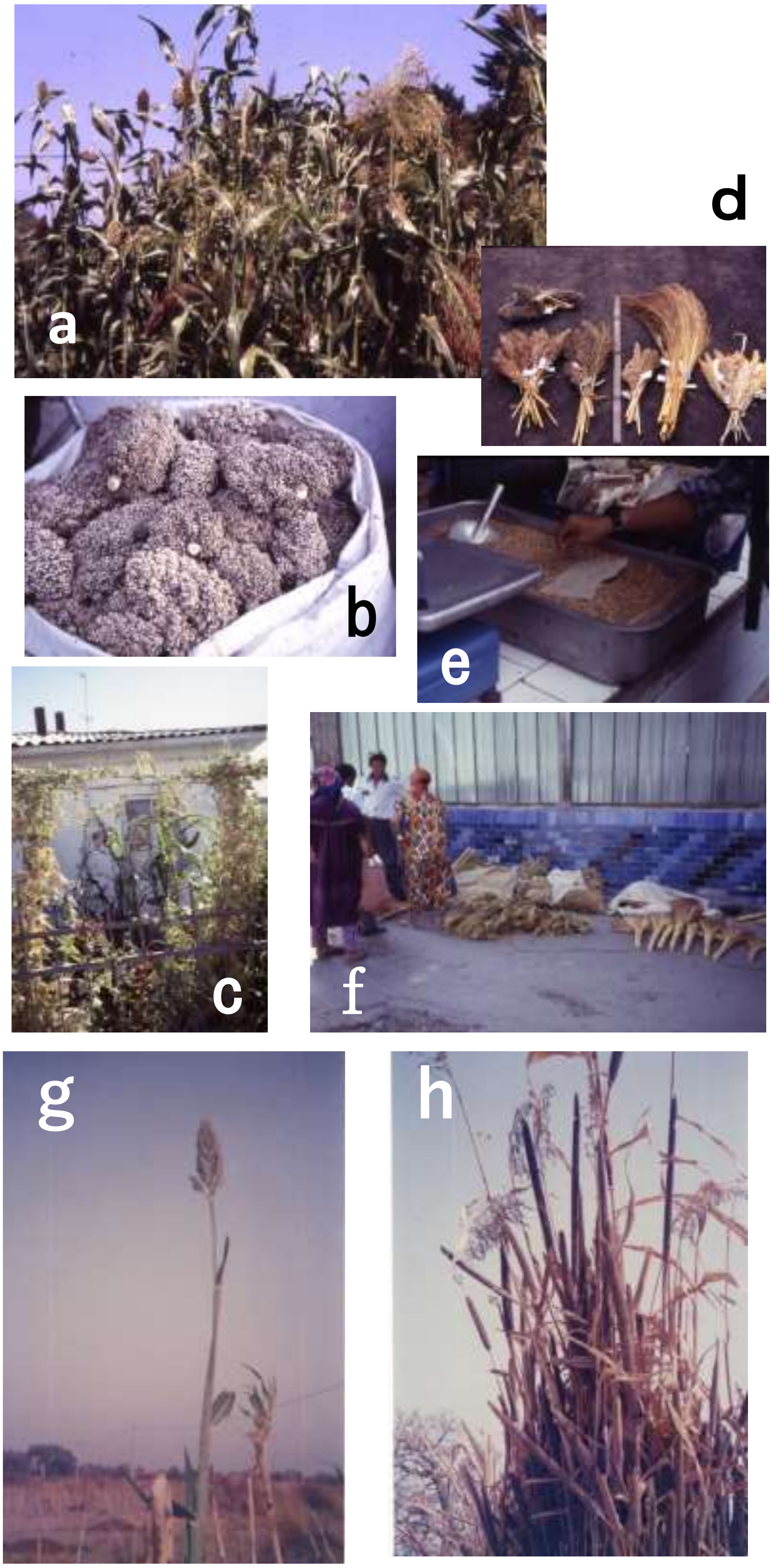


Figure 22. *Sorghum bicolor* in Central Asia and Africa

a, From India; b–f; Bazar in Central Asia; g and h, from Cote d’Ivoire, Africa (Konishi photo).

Polyploidy and growth habit of genus *Oryza*

The genus *Oryza* (Poaceae) comprises approximately 20 wild species and two domesticated species (Table 13). The group includes annual diploids (3 species), annual/perennial types (5 species), perennials (7 species), and perennial tetraploids (8 species) (Oka and Coworkers 1980, Morishima 2001).

Domesticated rice (*O. sativa*) is characterized as an annual/perennial diploid. Its ancestor, *O. rufipogon,* also displays annual and perennial growth habits and is native to tropical and subtropical regions of Asia (Figure 23). The speciation of these taxa is complex due to their significant diversity. *O. sativa* was originally domesticated from the wild perennial *O. rufipogon*. Through artificial section, *O. sativa* developed as an ecological annual, enhancing seed production via self-fertility. Notably, in regions with mild winters, plants can grow numerous ratoons post-harvest and flower again, indicating that, botanically, *O. sativa* retains perennial properties. Natural selection acts on habitat adaptation while farmers strongly influence the annual cultivation cycle through artificial selection. Moreover, upland rice has undergone secondary adaptation to arid environments and evolved an ecological annual growth habit in response to drought or cold conditions, optimizing the cultivation cycle within a year for farmers and plants.

O. glaberima Steud., native to West Africa, is an annual diploid domesticated from its ancestral species *O. barthii*, which is also an annual diploid. Another African wild rice species, *O. longistaminata,* is a perennial diploid exhibiting self-incompatibility, yet it propagates through seeds as well as subterranean stems.

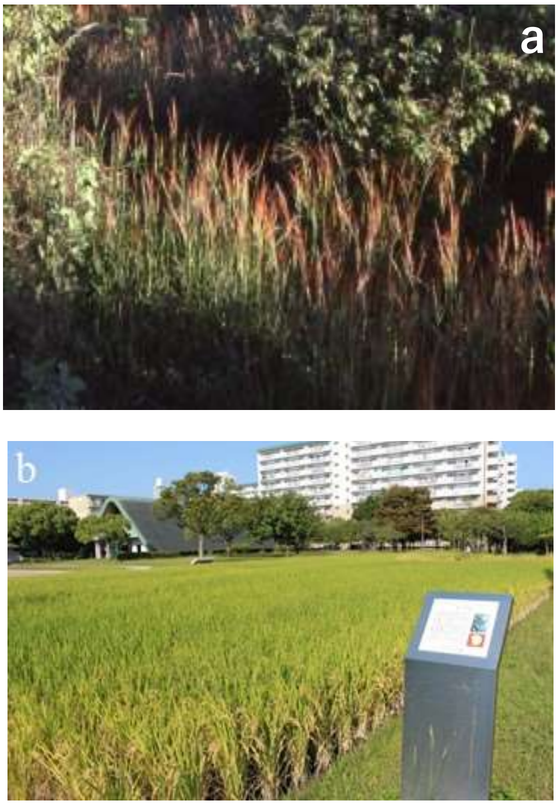


Figure 23. Rice paddy field

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

Table 13. Characteristics of genus *Oryza*

Genus *Oryza*	Chromosome number (2n)	Growth habit	Genome	Distribution
Section *Oryza*				
O. sativa *	24	A/P	AA	Global
***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.

Weeds as colonizing species

R. x brachyceras, while a sterile perennial, persists in its habitat through vegetative reproduction. This mode of reproduction is common among weedy *Rorippa* specie, reflecting their adaptation and colonization strategies in environments such as paddy fields. Generally, asexual reproduction systems (broadly considered as apomixis) are primarily found in perennial species, with only a few exceptions.

Among perennials, species like *Mazus miquelii* and *Cardamine lyrata* propagate extensively by producing ramets via stolons. Others—such as *C. sucutata*, *Coix lacryma-jobi* var. *lacryma-jabi*, the common form of *Agropyron tsukushiense* var. *transiens*, and *A. humidorum*—reproduce through regrowth from stumps and culms. In contrast, annuals including *M. japonicus*, *C. flexosa, C. impatiens*, the ecological annual *Coix lacryma-jobi* var *ma-yuen,* and the early ecotype of *A.*

tsykushiense var. *transiens,* do not reproduce asexually.

An annual plant completes its life cycle within 12 months, although its lifespan may span two calendar years if overwintering occurs. There are two primary categories of annual life cycles. The first ends abruptly with flowering and seed set, representing "true annuals" 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.

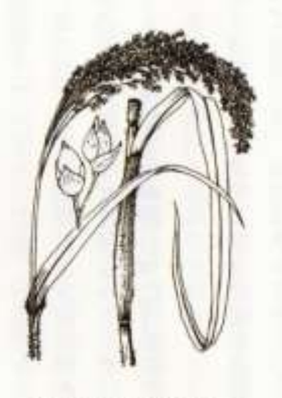
A comparative survey of herbaceous colonizing species identified three major colonizing types (Ehrendorfer 1965): perennial polyploids, annual self-pollinated, and annual diploid species. These types are observed in families such as Dipsacaceae, Asteraceae/Anthemideae, and Rubiaceae/Rubioideae. Each type demonstrates distinct evolutionary strategies with specific ecological roles, vegetative and reproductive traits, genetic systems, and population structures.

Stebbins (1950) further classified Gramineae species by their fertilization and growth habits, highlighting three general characteristics: (1) Annual species are relatively uncommon in cool temperature regions and predominant in warm, dry areas with seasonal rainfall; (2) annuals are almost exclusively self-pollinated, while perennials may be either cross- or self-fertilized; (3) Among perennials, rhizomatous types are almost exclusively self-incompatible and cross-fertilized, whereas caespitose, or "bunch-grass," species display varying degrees of self- and cross-fertilization.

Baker (1965) described weeds as colonizing species that typically exhibit an annual growth habit, broad environmental tolerance, and strong developmental homeostasis—enabling successful flowering and seeding under diverse conditions. Weeds also display notably plasticity in size in response to environmental variation. Baker (1974) subsequently proposed several ideal characteristics for weeds: (1) fulfillment of germination requirements in various environments; (2) discontinuous and internally controlled germination with seeds of great longevity; (3) rapid growth through the vegetative phase to flowering; (4) continuous seed production during favorable conditions; (5) self-compatibility without complete autogamy or apomixis; (6) utilization of generalist pollinators or wind for cross-pollination; (7) very high seed output in favorable environment circumstances; (8) the ability to produce seeds under a wide range of environmental conditions; (9) adaptations for short- and long-distance seed dispersal; (10) vigorous vegetative reproduction or regeneration in perennials; (11) brittle physical structure to avoid being easily removed from the ground; and (12) specialized means of interspecific competition, such as rosette formation, choking growth, or allelochemical production.

In colonizing species, the stages of germination and seedling establishment are critical for determining success or failure. The adaptive significance of germination polymorphism—variation in germination response to environmental factors such as light and temperature—has been emphasized for its role in enabling survival across varied conditions (Harper 1965; Cavers and Harper 1966; Shimizu and Tajima 1975).

Chapter 4 Domestication and dispersal of common millet (*Panicum miliaceum* L., Poaceae) in Eurasia



Panicum miliaceum L.
画 寺崎

Common millet (proso millet, *Panicum miliaceum* L.) has played a significant role in my ethnobotanical research. Reflecting on my own experiences, I recognize a deep-rooted connection to common millet that dates back to my childhood. This connection was fostered by family traditions: my grandfather's elder brother used to send our family two types of *mochi*—one made from waxy rice (white *mochi*) and the other from common millet (yellow *mochi*)—to our home in Nagoya. His paddy fields were located in Yagami, on the Nobi Plain, a region renowned for rice production due to the presence of the Kiso three rivers. Despite the prominence of rice cultivation in the area, a small amount of common millet was also grown on the uplands surrounding the rice paddies. I developed a fondness for the yellow *mochi*, especially when it was roasted and topped with soy sauce.

Domesticated species of genus *Panicum*

The genus *Panicum* (Poaceae) comprises approximately 500 species, many of which have been valued for their wild grains, as fodder, and medicinal properties throughout history. Among these, three cereal crops have been domesticated in various locations and periods: *P. miliaceum* L. (common millet), *P. sumatrense* Roth. (*samai* or little millet), and *P. sonorum* Beal. (saui or panic grass). These cereals are C_4 plants, characterized by robust drought resistance, early maturation, and high nutrient content.

P. sumatrense was domesticated from its ancestral species, *P. sumatrense* subsp. *psilopodium*, around 2200 BC on the Indian subcontinent (Weber 1992). *P. sonorum* was domesticated from *P. hirticaule* around 600 BC in northwestern Mexico (Nabhan and de Wet 1984). In contrast, common millet became the most important grain crop supporting Eurasia civilizations for thousands of years, beginning in the Neolithic era. Today, it remains widely cultivated and used in many parts of the world.

Although common millet is recognized as one of the oldest domesticated plants in Eurasia, the precise origins and ancestral plant have not been definitively identified. The question of its domestication and place of origin has been the subject of much debate among scholars (Bellwood 2005, Church 1886, de Candolle 1886, Gerard 1597, Harlan 1995, Jones 2004, Kimata 2009, Sakamoto 1987, Vavilov 1926). Vavilov (1926) proposed North China as the region of origin, while Chun et al. (2004) suggested that domestication occurred in the southern part of the middle reaches of the Yellow River 8000–7000 years BP.

Other hypotheses have been proposed: Harlan (1975) suggested two possible homelands—North China and eastern Europe—while Nesbitt (2005) argued that independent domestication could have occurred independently in each area. Despite these varying theories, the wild ancestor and precise domestication site of common millet remain unknown. Archaeological evidence shows the earliest presence of common millet as a crop in both Transcaucasia and China approximately 6000 BC. Zohary and Hopf (2000) suggested that common millet may have originated somewhere between the Caspian Sea and Xinjiang. The earliest sites bearing remains of common millet are in China and Europe, dating to the seventh millennium BC, placing its early cultivation on opposite ends of Eurasia (Jonse 2004). Additionally, Sakamoto (1987) indicated Central Asia and the northwestern Indian subcontinent as possible areas of origin. Common millet was found in Tepe Gaz Tavilla, in southeastern Iran, from the sixth millennium BC (Meadow 1986). One potential reason for its domestication may have been altered climate earlier in the Holocene. Meadow (1986) suggested that millet cultivation in dry regions could have been supported by floodwater runoff to supplement rainfall, allowing it to be grown as a spring or autumn crop. Similarly, in the Ganga region, common millet is sown after winter floods. Such localized analyses are crucial for understanding the origins and spread of common millet, particularly throughout Central Asia, a region vital to mapping the grain's historical diffusion (Hunt and Jones 2006). Despite these studies, the definitive ancestor and original homeland of common millet remain unclear.

Bellwood (2005) summarized current thinking on the origin and diffusion of common millet, drawing on recent archaeological findings. Common millet may have originated in Central Asia (Sakamoto 1987, Zohary and Hopf 2000), from where Neolithic settlers may have migrated to Afghanistan, the Russian steppes, and potentially western China. Common millet has been identified in Neolithic European cultures and across the Eurasian steppes, but the oldest confirmed cultivation dates are from North China, beginning around 6500 BC. The first known appearance in southeastern Iran dates to the sixth millennium BC (Meadow 1986), c. 1550 BC in northwestern Iran (Nesbitt and Summers 1988), and approximately 2600 BC in South Asia (Fuller et al. 2001).

Morphological characteristics

The heading of common millet often occurs irregularly due to the panicle flowering inside the leaf sheath 4–5 days before heading. As a result, the duration (days) from sowing to flowering is observed instead of the heading date. Generally, local varieties from high latitude regions exhibit a brief flowering period, though the number of days varies remarkably. Varieties from China, Mongolia, the former USSR, Europe, and Japan (specifically Hokkaido) flower very early, often by 40 days after sowing, whereas varieties from India and southern Japan tend to flower later, with approximately one-third flowering by 80 days. Furthermore, varieties from China, Mongolia, the former USSR, Europe, and Japan (Hokkaido) have fewer leaves (5–10) on the main culm compared to those from southern and western Asia, Korea, and southern Japan, which have 11 to 16 leaves.

All varieties from Japan, Korea, and Nepal possess only a few productive tillers (1 to 3). In contrast, varieties from southern and western Asia, the former USSR (including Central Asia), and

Europe display broader variation (1–6 tillers), with some Indian samples reaching up to of 9 tillers (6.9%).

Common millet is a densely piliferous plant. The hairiness of the uppermost internode can be categorized into four types: glabrous, sparse, moderate, and dense. While most varieties are glabrous or sparse, dense hairiness is more prevalent in Hokkaido (40.0%), western Asia (26.1%), and Europe (20.0%).

The panicle of common millet is divided into five types: sparse, dense, compact, and two intermediate forms (Kimata 2016). Most local varieties from Japan (Hokkaido), China, India, western Asia, the former USSR, and Europe are of the sparse type, while those from Japan, Korea, and Nepal are dense. Few varieties from western Asia, the former USSR, and Europe are classified as compact.

On mature plants, lemma color is classified into six colors: dark brown, brown, pale brown, ivory, orange, and grayish-green. Varieties from the former USSR and Europe show considerable variations in color. Most grains from Japan (Hokkaido) and China are dark brown, while grains from southern Japan range from brown to ivory. In India, grayish-green grains are common (45.6%), along with pale brown and ivory. Stigma color of the pistil at maturity is either white, faint purple, or purplish-red. Approximately 70% of varieties exhibit white or faint purple stigmas. In southern Japan and Nepal all varieties except one have white stigmas, whereas purplish-red stigmas predominate in Japan (Hokkaido), India, and western Asia (over 73%). In Europe, 28% of varieties show purplish-red stigmas (Kimata 2016).

Partial correlation coefficients for 14 morphological characteristics reveal that coefficients greater than 0.6 (at a 1% significance level) are observed for plant height (PH) and number of leaves (LN) on the main culm to days for flowering (DF; Table 14). Additionally, DF, LN, flag leaf length (FL), flag leaf width (FW), and diameter of uppermost internode (DI) are correlated with PH; DF, PH, FW, and DI correlate with LN; PH, LN, FL, and FW correlate with each other and with DI. However, characteristics such as number of tillers (TN), panicle length (PL), panicle type (PT), lemma color (LC), stigma color (SC), hairiness of uppermost internode (PI), and shattering (SH) are not highly statistically significant. Domestic varieties with late maturity are generally tall with many leaves, a large flag leaf for effective photosynthesis, and a robust culm supporting a heavy panicle.

Table 14. Partial correlation coefficients of 14 characteristics

	Days for flowering	No. of tillers	Plant height	No. of leaves on main culm	Length of flag leaf	Width of flag leaf	FL/FW	Panicle length	Diameter of uppermost internode	Panicle type	Lemma color	Stigma color	Hairiness of uppermost internode	Shattering
DF	1.000	0.005	0.835**	0.916**	0.501**	0.503**	-0.032	-0.400**	0.569**	0.363**	-0.055	0.131	0.078	0.027
TN	0.005	1.000	-0.203	-0.173	-0.216	-0.347**	0.297*	-0.259	-0.375**	-0.157	-0.118	-0.045	-0.008	-0.048
PH	0.835**	-0.203	1.000	0.907**	0.746**	0.736**	-0.095	-0.024	0.804**	0.543**	-0.030	0.015	0.036	0.057
LN	0.916**	-0.173	0.907**	1.000	0.594**	0.640**	-0.145	-0.310*	0.713**	0.372**	-0.009	0.172	0.056	0.066
FL	0.501**	-0.216	0.746**	0.594**	1.000	0.787**	0.164	0.179	0.726**	0.382**	0.039	-0.012	0.049	0.221
FW	0.503**	-0.347**	0.736**	0.640**	0.787**	1.000	-0.451**	0.170	0.814**	0.515**	-0.127	-0.123	-0.104	0.186
FL/FW	-0.032	0.297*	-0.095	-0.145	0.164	-0.451**	1.000	-0.052	-0.254	-0.226	0.217	0.123	0.202	0.002
PL	-0.400**	-0.259	-0.024	-0.310	0.179	0.170	-0.052	1.000	0.169	0.235	0.061	-0.240	0.052	-0.116
DI	0.569**	-0.375**	0.804**	0.713**	0.726**	0.814**	-0.254	0.169	1.000	0.548**	-0.033	-0.079	0.082	0.081
PT	0.363**	-0.157	0.543**	0.372**	0.382**	0.515**	-0.226	0.235	0.548**	1.000	-0.043	-0.335	-0.128	-0.142
LC	-0.055	-0.118	-0.030	-0.009	0.039	-0.127	0.217	0.061	-0.033	-0.043	1.000	0.358	0.102	0.043
SC	0.131	-0.045	0.015	0.172	-0.012	-0.123	0.123	-0.240	-0.079	-0.335*	0.358**	1.000	0.124	-0.011
HI	0.078	-0.008	0.036	0.056	0.049	-0.104	0.202	0.052	0.082	-0.128	0.102	0.124	1.000	0.053
SH	0.027	-0.048	0.057	0.066	0.221	0.186	0.002	-0.116	0.081	-0.142	0.043	-0.011	0.053	1.000

Controlled value is Iodine color reaction; * 5%, ** under 1% level significance.

Hierarchical cluster analysis, illustrated using the group average method of SPSS, of eight morphological characteristics and earliness, divides 75 local varieties into two major clusters, I, with five sub-clusters, and II, with two sub-clusters. Sub-cluster Ia comprises 11 varieties, from Central Asia (3 varieties, former USSR), Uzbekistan (1), China (3), Spain (1), Germany (2), and Canada (1). Sub-cluster Ib is primarily from Western Europe, with some from Japan (Hokkaido), Mongolia, Uzbekistan, and Pakistan. Sub-cluster Ic contains mostly Eastern European varieties, as well as some from Uzbekistan and the Indian subcontinent. Sub-cluster Id comprises three varieties from Afghanistan, Greece, and Pakistan, while Ie comprises one variety from India. Sub-cluster IIa includes 20 varieties, primarily from East Asia, with a few from Nepal (3) and Bulgaria (1); IIb comprises 11 varieties from the Indian subcontinent, as well as a select few from China (2), Japan (2), and Romania (1). The distribution of morphological characteristics generally reflects two geographical trends: one from Central and South Asia toward Europe via Asia Minor, and another from China toward India (via Nepal) and Japan (via Korea) to the far east.

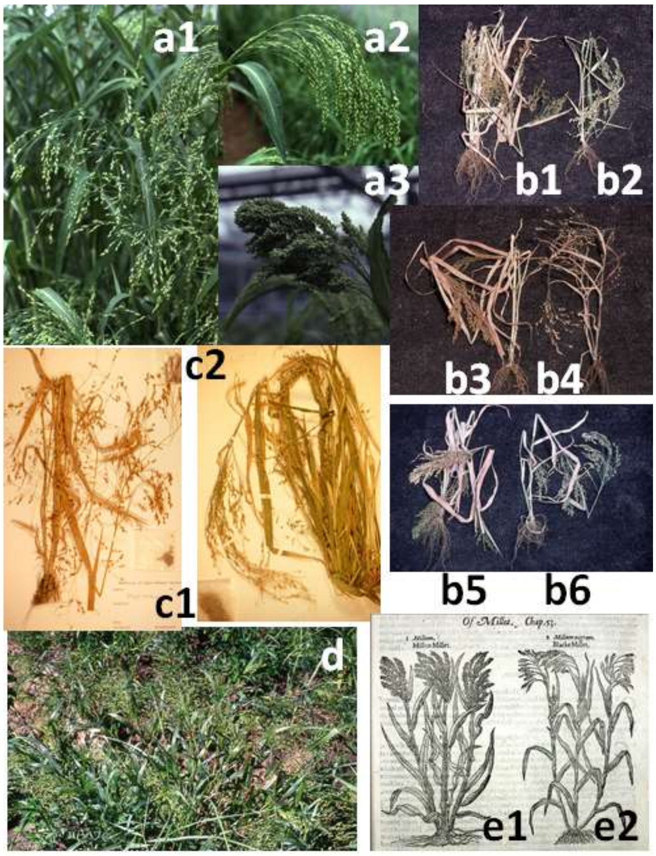


Figure 24. Morphology of common millet, *P. miliaceum*.
Types of panicle: a1, sparse; a2, compact; a3, dense. Domestic type and mimic weed in Central Asia: b1, b3 and b5, subsp. *miliaceum*; b2, an escaped weed; b4 and d, subsp. *ruderale*; and b6, subsp. *agricolum*. c1, a crop-like weedy biotype in Pakistan and c2, a F_1 hybrid between subsp. *miliaceum* and subsp. *ruderale*. e1/e2, *P. miliaceum* cultivated in Europe, about 17 century (Gerarde 1597).

Figure 24 illustrates typical panicle types: sparse (a1), compact (a2), and dense (a3). It also shows a domestic (b1) and escaped weed (b2) type in Pakistan; a domestic (b3) and weed, ssp. *ruderale* (b4) in Romania; a domestic (b5) and weed subsp. *agricolum* (b6) in Uzbekistan; a crop-like weedy biotype, subsp. *miliaceum* (c1); and an F1 hybrid between a domestic type and the subsp. *ruderale* in Pakistan (c2), with both sparse and shattering panicles. It also shows a weed, subsp. *ruderale*, in Inner Mongolia (d, taken in 2004) and European common millet (e1 and e2) illustrated in a book (Gerarde 1597). The panicles of common millet can be divided into five types: sparse, compact, dense, and two intermediate types (relatively sparse or dense). Common millet is generally a densely piliferous plant, but the hairiness of the uppermost internode is highly variable. This trait can be divided into four types: glabrous, sparsely, moderately and densely piliferous.

Lyssov (1968, 1975) classified *P. miliaceum* L. into five groups based on panicle types (Figure 25): race *miliaceum* (similar to wild species); race *patentissimum* (long, slender, sparse panicles; a1) distributed from Eastern Europe to Japan; race *contractum* (droopy, compact panicle; a2); race *compactum* (cylindrical, erect panicle); race *ovatum* (oval, dense panicle; a3). These morphological groupings do not demonstrate distinct geographical clines and do not directly reflect taxonomic relationships. The taxonomy of common millet requires identification of intra-specific differentiation using a matrix of various traits. Scholz and Mikolāš (1991) further classified *P. miliaceum* into three subspecies: *miliaceum*, *ruderale*, and *agricolum*. Subsp. *miliaceum* includes the cultivar form (b1, b3, b5) and crop-like weedy biotype (c1) found in Pakistan, Austria, Slovakia, and Canada, respectively. Subsp. *ruderale* (b4, d) is an escaped weed from subsp. *miliaceum* (b2) with small grains that shatter easily on its sparse panicle and is found worldwide. Subsp. *agricolum* (b6) is a mutant race with intermediate characteristics between the domestic form and subsp. *ruderale*, notable for its strong herbicide tolerance and occurrence in maize fields. The two types of European common millet from the sixteenth century may correspond to races *ovatum* (e1) and *patentissimum* (e2). Additionally, F_1 hybrids (c2) between subsp. *miliaceum* and subsp. *ruderale* have been observed.

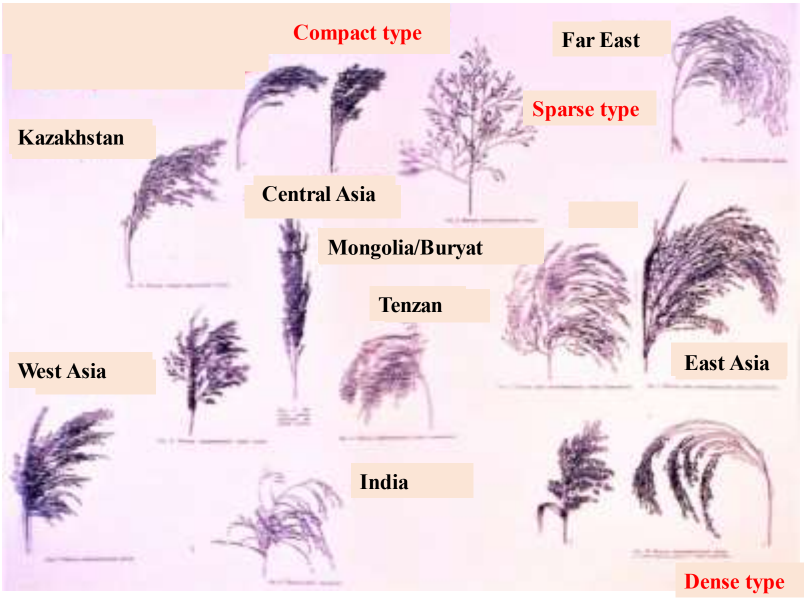


Figure 25. Spike variation of *P. miliaceum* in Asia

Lyssov (1968, 1975) modified

Variation of common millet in Hokkaido, North Japan

Since 1974, we have conducted field studies on common millet (*P. miliaceum*) in the Kanto Mountains of Central Japan (Kimata et al. 1978, Kimata et al. 1979, Kimata and Yokyama1982), and expanded to Hokkaido in Noth Japan from 1981 (Kimata *et al*. 1986, 1995, 1996, 1997), largely influenced by the presence of the Ainu people, who continue to cultivate *P. miliaceum*, *Echinochloa utilis,* and *Setaria italica*. Visits to farmers in South Hokkaido, particularly along the Saru river at Biradori, revealed that traditional varieties of millet are maintained by the Ainu (Figure 26). Seeds were collected from local farmers for detailed analysis, including 14 accessions from Saru river, one from Oshima peninsula, and one from Sharicho.

The 14 local varieties from Biradori underwent cultivation tests to assess their morphological characteristics (Table 15). Through the combination of seven key traits—maturity, number of tillers, spikelet-to-spike length ratio, 1000-grain weight (g), glume color, empty glume color, and hairiness on the spike neck—these accessions were categorized into eight types (Kimata *et al*. 1986). Types A (6 accessions) and B (2 accessions) demonstrated the features of typical indigenous varieties:

early maturity, few tillers, low spikelet-to-spike length ratio, heavier 1000-grain weight, dark brown glume, red-purple empty glume, and pronounced hairiness on the spike neck when cultivated in Tokyo.

Other types showed evidence of adaptation to local environments, particularly in Hidaka, likely due to introduction from Honshu during the Meiji period and subsequent natural or artificial crossbreeding. These types presented late maturation, orange glume, and glabrous spike necks, indicating diverse variation shaped by selection pressures.

Comparative field experiments by Noboru Tachibana in 1984, involving varieties from Kanto, Hokuriku, and Hokkaido, showed that plant height varied, but other stable traits—such as red-purple empty glume and more hairiness on the neck of spikes—remained consistent across locations.

The spike types among the Hokkaido varieties included compact (8 strains), sparse (4 strains) and dense (2 strains). Iodo-starch reactions of the albumen starch from all strains (total 14) yielded a grape color, indicating a medium starch type between waxy and non-waxy, and suggesting polyploidy (Table 16).

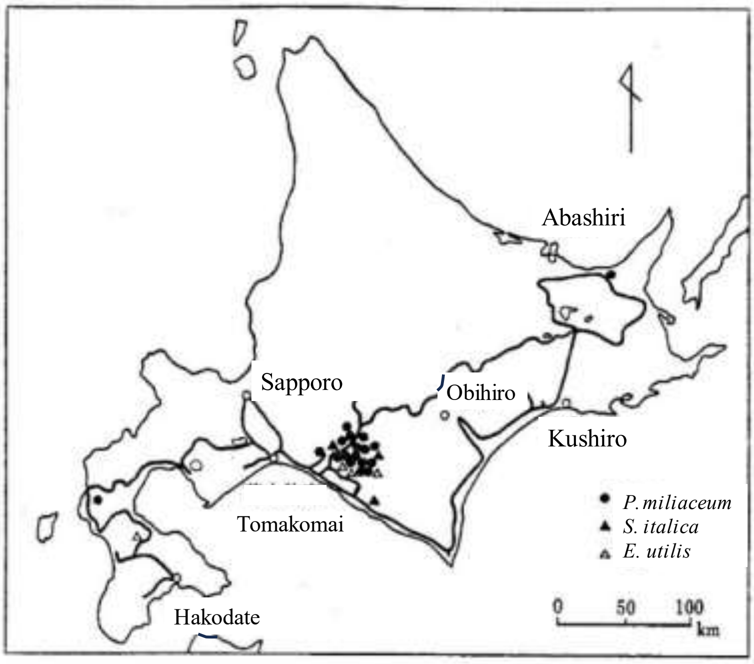


Figure 26. Field survey route and distribution sites of millet (1981–1984)

Table 15. Characteristics of *P. miliaceum* from Biratori and others in Hokkaido

Type	A	B	C	D	E	F	G	H
Characteristics								
Maturity	early	early	early	early	medium	medium	Late	Late
Tillers	a few	a few	many	a few	a few	a few	many	a few
Spiklets/Spike Length rate	a few	a few	a few	a few	many	a few	many	many
1000 grains (g)	medium	heavy	medium	light	light	medium	light	light
Glume color	dark brown	dark brown	dark brown	dark brown	dark brown	orange	dark brown	orange
Empty glume color	red purple	red purple	red purple	green	green	green	green	red purple
Heiriness on neck of spike	hairy	many	many	hairy	many	hairy	hairless	hairy
No. of strains	6	2	1	1	1	1	1	1

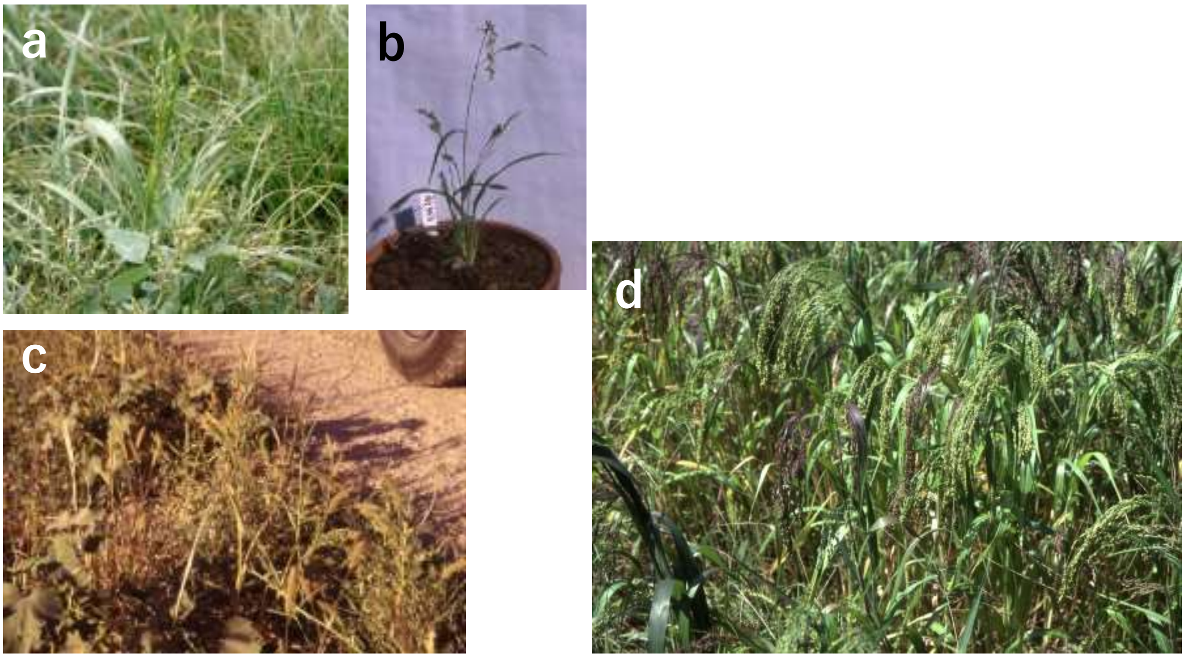


Figure 27. Wild and domesticated types of *Panicum miliaceum*

a, Wild type, *P. miliaceum* ssp. *ruderale* in Inner Mongolia; b, local variety C type of Osachinai, Hokkaido cultivated at Koganei, Tokyo; c, escaped type on the roadside near Tashkent, Uzbekistan; d, local variety (purple spike) and introduced variety (green spike) on a mix-sowing field at Hobetsu, Hokkaido,

Table 16. Geographical variation of *P. miliaceum* in Eurasia

Locality Characteristics	Japan Hokkaido	 South of Honshu	East/South Asia	West/Central Asis	Europe
Headinng days	early	medium/late	medium/late	medium/late	medium
No. of leaves	a few	medium/many	medium	a few/medium	a few
Plant height	short	medium/long	medium/long	medium/long	short
No. of tilers	a few	medium	medium	a few/many	a few
No. of spikelets	a few	medium/many	medium	a few/medium	a few
1000 grains (g)	light/heavy	light/lighter	heavier	heavier	light/heavier
Glume color	dark brown	dark brown/orange/white	dark brown/orange/white	orange/white	white
Empty glume color	red purple(green)	green	green	red purple/green	red purple
Heiriness on neck of spike	hairy	glabrous	glabrous	hairy	many

Crossability among Eurasian varieties and morphological characteristics of F_1 hybrids

Crossability tests among six pollen testers were conducted by artificial crossing of florets (range: 5–50, mean: 17) on panicles (range: 1–3, mean: 1.2), yielding an average fructification rate of 4.8%. A total of 351 combinations produced 117 F_1 hybrids. The process was technically challenging due to irregular flowering and sensitivity to weather, particularly anther dehiscence under wet conditions. Crossability ranged from 0 to 63.9%, with F_1 hybrids obtained from 18 varieties. Ovum parents generally had lower crossability than pollen parents. Of the F_1 hybrids, seeds from 105 strains were tested for germination. Most germinated well, but some failed necrotized immediately after germination. All F_1 hybrid plants exhibited high pollen fertility, exceeding 78%.

Crossability rates varied by region (Table 7). The French tester produced the most fertile F_1 plants (41.2%) with European varieties; the Central Asian tester succeeded (58.8%) primarily with East Asian varieties but was infertile when crossed with Indian or Chinese ovum parents, similar to when crossed with a weed (p32); the Indian tester with East (33.3%) and South (30.8%) Asian varieties; the Chinese tester (p51) with East Asian (45.0%) and European (45.0%) varieties; the Japanese tester (p60) with East Asian (45.0%), Central Asian (37.6%), and South Asian (38.9%) varieties; and the weed tester (p32, subsp. *ruderale* from Romania) with South (35.7%) and Central (28.6%) Asian varieties. Notably, subsp. *ruderale* pollen could artificially fertilize the ovum of domestic varieties, though reciprocal crosses failed. Notably, a domestic variety with sparse and shattering panicles (PC57-2 from Hokkaido, Japan) produced F_1 hybrids with testers from Central Asia, India, and Japan.

Table 17. Crossability (%) among local varieties

Ovum	No. of varieties	Pollen					
Locality		France	p32 Weed	Central Asia	India	p51 China	p60 Japan
East Asia	21	23.5	16.7	58.8	33.3	45.0	45.0
Central Asia	8	16.7	28.6	20.0	0	0	37.6
South Asia	19	26.7	35.7	29.4	30.8	25.0	38.9
Europe	20	41.2	16.7	17.6	17.6	45.0	21.1
Canada	1	0	0	+	0	0	0
Weed type (Romania)	1	0	0	0	0	0	0
Total combinations	70	56	58	47	65	67	58

+, with another variety.

These data suggest that common millet likely dispersed from Central Asia to China and Europe, and then indirectly to South Asia and East Asia. The weed (p32) was reproductively isolated as an ovum parent but could fertilize other varieties as a pollen parent, suggesting that subsp. *ruderale* was a possible ancestor due to its ability to produce fertile F_1 hybrids between the other varieties.

F_1 hybrids inherited panicle types from their testers: hybrids with sparse-panicled Indian testers remained sparse, while those with dense-panicled Japanese testers (p60) exhibited panicle types matching the parental density. Middle-type panicles were generally retained in hybrids from parents with intermediate panicle types.

Common millet is generally a densely piliferous plant, but the hairiness of the uppermost internode is highly variable: glabrous, sparse, moderate, and dense. F_1 hybrids between moderate varieties (e.g., p9, p11, and p56) generally have moderate internodes, except p8 (glabrous). F_1 hybrids with the glabrous testers from Central Asia, China, and Japan predominantly have a glabrous internode, excluding p2, p53, and p9 (moderate). F_1 hybrids between the moderate or dense varieties and the dense Indian tester vary widely between glabrous, sparse, and moderate, while an F_1 hybrid between a glabrous variety from Japan (Hokkaido) and the moderate Indian tester has a glabrous internode.

Variation in Central Asian common millet

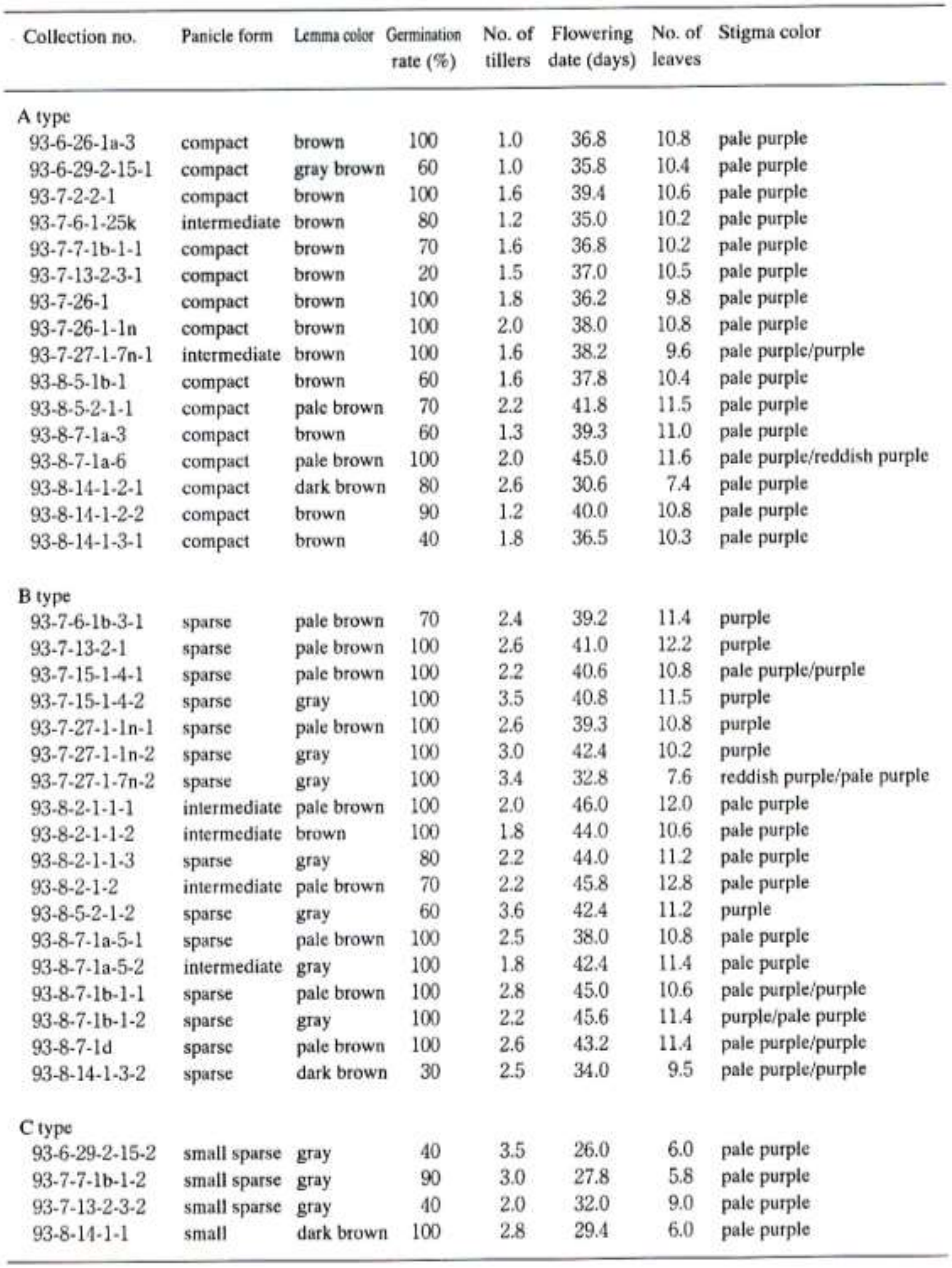
Examination of Central Asian common millet revealed considerable diversity in several morphological and ecological traits (Table 18). The panicle form is generally classified into three types: A, compact; B, sparse; C, small sparse. Despite these broad categories, detailed observations indicate remarkable variation within each type.

Lemma color among the accessions was organized into four grades: pale brawn, brown, dark brawn, and gray. Seed germination rates were predominantly high, with most accessions exhibiting rates over 60%, excluding five accessions. The average number of tillers per plant varied considerably from 1.0 to 3.6. Flowering dates were relatively short, spanning 26.0 to 40.6 days. The number of leaves on the main culm was generally small, ranging from 5.8 to 12.2. Stigma color could be separated into three categories: pale purple, purple, and reddish purple.

Specific trait combinations were noted for each panicle type. Most accessions with compact panicles (Type A) have brown lemma, produce few tillers, flower in the middle of the observed range, and display pale purple stigmas. Accessions with sparse panicles (Type B) typically exhibit pale brown or gray lemma, have relatively more tillers, share a middle flowering date, and have purple stigmas. Notably, the characteristics of Type B closely resemble those observed in the landraces of Hokkaido (North Japan). These parallels are significant for understanding possible northern dispersal routes into Japan.

Type C, characterized by small sparse panicles, correspond to an associated mimic weed, *P. miliaceum* ssp. *ruderale* (Kitag.) Tzvelev. These accessions feature grayish lemma, relatively more tillers, early flowering date, fewer leaves on the main culm, and pale purple stigmas. Additionally, Type C plants exhibit pronounced seed shattering and deep dormancy—traits typical of weedy plants. Collectively, these data support the hypothesis that West Turkestan was a center of domestication for common millet, and that the weed form, *P. miliaceum* ssp. *ruderale*, may have been an ancestor of cultivated common millet.

Table 18. Several characteristics of common millet cultivated in Tokyo, Japan



Collection no.	Panicle form	Lemma color	Germination rate (%)	No. of tillers	Flowering date (days)	No. of leaves	Stigma color
A type							
93-6-26-1a-3	compact	brown	100	1.0	36.8	10.8	pale purple
93-6-29-2-15-1	compact	gray brown	60	1.0	35.8	10.4	pale purple
93-7-2-2-1	compact	brown	100	1.6	39.4	10.6	pale purple
93-7-6-1-25k	intermediate	brown	80	1.2	35.0	10.2	pale purple
93-7-7-1b-1-1	compact	brown	70	1.6	36.8	10.2	pale purple
93-7-13-2-3-1	compact	brown	20	1.5	37.0	10.5	pale purple
93-7-26-1	compact	brown	100	1.8	36.2	9.8	pale purple
93-7-26-1-1n	compact	brown	100	2.0	38.0	10.8	pale purple
93-7-27-1-7n-1	intermediate	brown	100	1.6	38.2	9.6	pale purple/purple
93-8-5-1b-1	compact	brown	60	1.6	37.8	10.4	pale purple
93-8-5-2-1-1	compact	pale brown	70	2.2	41.8	11.5	pale purple
93-8-7-1a-3	compact	brown	60	1.3	39.3	11.0	pale purple
93-8-7-1a-6	compact	pale brown	100	2.0	45.0	11.6	pale purple/reddish purple
93-8-14-1-2-1	compact	dark brown	80	2.6	30.6	7.4	pale purple
93-8-14-1-2-2	compact	brown	90	1.2	40.0	10.8	pale purple
93-8-14-1-3-1	compact	brown	40	1.8	36.5	10.3	pale purple
B type							
93-7-6-1b-3-1	sparse	pale brown	70	2.4	39.2	11.4	purple
93-7-13-2-1	sparse	pale brown	100	2.6	41.0	12.2	purple
93-7-15-1-4-1	sparse	pale brown	100	2.2	40.6	10.8	pale purple/purple
93-7-15-1-4-2	sparse	gray	100	3.5	40.8	11.5	purple
93-7-27-1-1n-1	sparse	pale brown	100	2.6	39.3	10.8	purple
93-7-27-1-1n-2	sparse	gray	100	3.0	42.4	10.2	purple
93-7-27-1-7n-2	sparse	gray	100	3.4	32.8	7.6	reddish purple/pale purple
93-8-2-1-1-1	intermediate	pale brown	100	2.0	46.0	12.0	pale purple
93-8-2-1-1-2	intermediate	brown	100	1.8	44.0	10.6	pale purple
93-8-2-1-1-3	sparse	gray	80	2.2	44.0	11.2	pale purple
93-8-2-1-2	intermediate	pale brown	70	2.2	45.8	12.8	pale purple
93-8-5-2-1-2	sparse	gray	60	3.6	42.4	11.2	purple
93-8-7-1a-5-1	sparse	pale brown	100	2.5	38.0	10.8	pale purple
93-8-7-1a-5-2	intermediate	gray	100	1.8	42.4	11.4	pale purple
93-8-7-1b-1-1	sparse	pale brown	100	2.8	45.0	10.6	pale purple/purple
93-8-7-1b-1-2	sparse	gray	100	2.2	45.6	11.4	purple/pale purple
93-8-7-1d	sparse	pale brown	100	2.6	43.2	11.4	pale purple/purple
93-8-14-1-3-2	sparse	dark brown	30	2.5	34.0	9.5	pale purple/purple
C type							
93-6-29-2-15-2	small sparse	gray	40	3.5	26.0	6.0	pale purple
93-7-7-1b-1-2	small sparse	gray	90	3.0	27.8	5.8	pale purple
93-7-13-2-3-2	small sparse	gray	40	2.0	32.0	9.0	pale purple
93-8-14-1-1	small	dark brown	100	2.8	29.4	6.0	pale purple

Materials and Methods for several experiments

A series of studies was initiated to investigate the morphological and ecological characteristics of common millet, followed by analyses of secondary compounds in the grain (Kimata and Negishi 2002, Kimata et al. 2007), with a particular focus on clarifying the ancestor, domestication process, and geographical dispersal of common millet in Eurasia. To address these question, a variety of botanical characteristics were integrated, including biocultural diversity (e.g., traditional food styles and archeolinguistic data) and genetic features (crossability, F_1 hybrids and AFLP markers).

Since 1973, extensive field surveys across Japan and the Eurasian continent have yielded a substantial collection of endemic *Panicum miliaceum* L. varieties and their relatives. Grain samples (650 accessions) were collected along the survey route, with voucher herbarium specimens deposited at Tokyo Gakugei University (Tokyo, Japan). Agricultural practices, grain processing methods, food preparation techniques, and vernacular names was also recorded from local farmers.

A subset of 441 local varieties was selected for comparative morphological and ecological analysis in the greenhouse at Tokyo Gakugei University, starting on July 10, 1986. These included 132 accessions from Japan, 39 from eastern Asia, 78 from the former USSR, 90 from southern Asia, 26 from western Asia, 43 from Europe, 2 from Africa, and 1 from Canada (Kimata and Negishi 2002).

For planting, ten grains from each strain were sown in seeding boxes with a row spacing of 8 cm and seed spacing of 2 cm. After two weeks, germinated seedlings were transplanted into the greenhouse, with 30-cm row spacing and 15 cm between plants. Chemical fertilizer (N:P:K = 8:8:5) was supplied at 100 $g \cdot m^{-2}$. Five plants from each strain were measured for traits, including duration to flowering (days), number of leaves on the main culm, number of productive tillers, hairiness of the uppermost internode, panicle type, lemma color, pistil stigma color, and other characteristics. The resulting data were analyzed using partial correlation coefficients and hierarchical cluster analysis.

In addition, 70 local varieties—including six pollen testers—were cultivated in the greenhouse from 1990 to 1995. These accessions represented 21 from eastern Asia, 8 from Central Asia, 19 from southern Asia, 21 from Europe, and 1 weed form, *P. miliaceum* subsp. *ruderale*, from Romania. The crossability among the 70 Eurasian varieties and morphological characteristics of their F_1 hybrids were examined in the six pollen testers from France, Central Asia, India, China, Japan, and the weed form.

Ten grains from each of the 75 accessions were sown on October 4, 2007, following the methodology described above (Table 19). DNA was extracted from young leaf tissue, which was ground in liquid nitrogen and incubated in 1.5-mL tubes containing 0.5 mL of buffer A for 10 min at 60 °C using the CTAB (hexadecyl-trimethyl-ammonium bromide) methods (Murray and Thompson 1980). The amplified fragment length polymorphism (AFLP) procedure was performed according to protocols established by Applied Biosystems (2005), Bai et al. (1999), and Suyama (2001), with some modifications.

Amplification reactions utilized five *Eco*RI-associated primers (E+AAC, E+AAG, E+AGG, E+ACT, and E+ACA) in combination with five *Mse*I-associated primers (M+CAG, M+CTG, M+CTA, M+CAT, and M+CAA). Five microliters of each amplification product were loaded onto a 5.75% denaturing polyacrylamide gel (LONZA) and subjected to electrophoresis in 1× TBE for 1 h. Bands were visualized using the silver staining method described by Cho et al. (1996). The gel bands were detected with Lane Analyzer (ATTO) at the highest sensitivity, and the resulting raw data were adjusted accordingly. Visible and reproducible bands were scored for each accession as present (1) or absent (0).

The dendrogram of AFLP markers was constructed using neighbor-joining and UPGMA methods (Nei and Kumar 2000), incorporating bootstrap analysis (PAUP* ver. 4.0) and hierarchical cluster analysis (group average method, SPSS ver. 21) on the complete data matrix for all 75 local varieties.

Table 19. Materials of *P. miliaceum* and related species

Area collected	Sample no.	Total
Japan	p1, p2, p30, p37, p38, p39, p60	7
Korea	p3, p4, p23,	3
China	p5, p14, p15, p19, p29, p51	6
Mongolia	p18, p20,	2
Nepal	p13, p16, p52	3
Bangladesh	p50	1
Uzbekistan	p68, p69, p70	3
Afghanistan	p6, p7,	2
India	p53, p54, p55, p56, p57, p61; (*P. sumatrense*) pm2, pw1, pw68	9
Pakistan	p58, p59,pp62, p63, p64, p65, p66, p67	8
Turkey	p17, p33, p91 (weed)	3
Greece	p36,	1
Romania	p9, p10, p24, p31, p32, p34, p35	7
Czechoslovakia	p21	1
Yugoslavia	p40	1
USRR-E	p41, p43, p46, p49	4
USSR-CA	p42, p45, p48	3
Poland	p44	1
Bulgaria	p22	1
Germany	p25, p26, p27, p28,	4
Belgium	p8	1
France	p11	1
Spain	p12	1
Canada	p47	1
USA	(*P. sonorum*) p111	1
Total		75

Phylogenetic analysis by AFLP markers

The phylogenetic relationships among 75 local varieties of *P. miliaceum, P. sumatrense*, *P. sonorum*, and its relatives were elucidated using AFLP markers. The data were analyzed with PAUP* version 4.0 and SPSS version 21, employing neighbor-joining and UPGMA methods with bootstrap tests (Figure 28). Distinct interspecific differentiation was observed among domestic and weed types of *P. miliaceum* from Pakistan and Uzbekistan, as well as between *P. sumatrense* and *P. sonorum* during the bootstrap analysis. However, intraspecific differentiation among common millet varieties was less pronounced in the bootstrap test (200 replicates; UPGMA tree, PAUP*). Despite this, a geographical trend was apparent in the dendrogram. The 75 varieties were grouped into two major clusters: Cluster I with six sub-clusters, and Cluster II comprising three sub-clusters.

Sub-cluster Ia included five varieties from Germany, Romania (subsp. *ruderale*), China, and Japan (two varieties) as illustrated in Figure 29. Sub-cluster Ib contained seven varieties from Turkey, Greece, Romania (2), and Japan (3). Sub-cluster Ic1 consisted of six varieties from Yugoslavia, the European portion of the former USSR (USSR-EU, 2), the Central Asian region of the former USSR (USSR-CA, 2) and Poland. Sub-cluster Ic2 included ten varieties from Canada, USSR-EU (2), USSR-CA, China, Nepal, Bangladesh, and India (3). Sub-cluster Ic3 comprised eight varieties from India (3), Pakistan (4), and Japan. Sub-cluster Id contained seven varieties from Pakistan (4, with two weed types) and Uzbekistan (3, with one weed type). Sub-cluster IIa featured two varieties from

Afghanistan; IIb comprised nine varieties from China (2), Nepal (2), Romania (2), France, Spain, and Belgium; IIc consisted of 11 varieties from China, Korea, Mongolia (2), Turkey, Bulgaria, Romania, Czechoslovakia, and Germany (3).

The AFLP marker distribution revealed two primary geographical patterns: one from Afghanistan and Mongolia toward Europe and Nepal via China (west and east), and another from Uzbekistan and Pakistan toward India and Eastern Europe via USSR-CA/EU (south and west).

Using hierarchical cluster analysis (group average method, SPSS), 51 varieties were grouped into two clusters. Cluster I comprised five varieties, including three weed types from Pakistan and Uzbekistan; Cluster II contained 46 varieties from other regions.

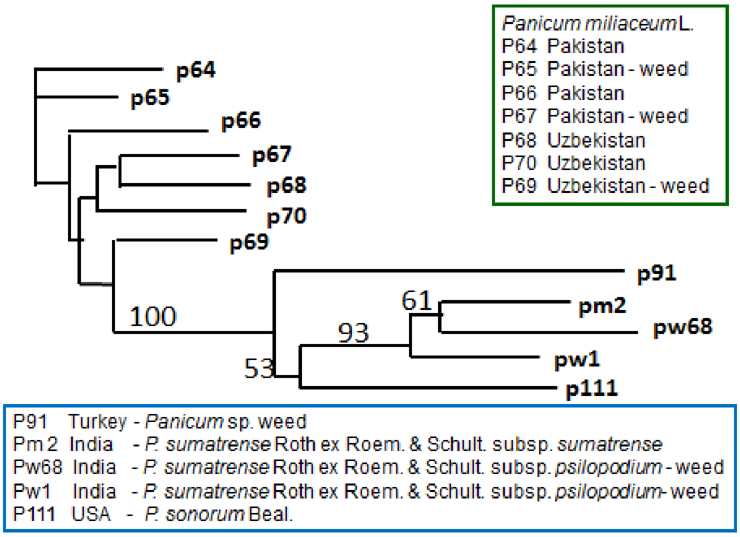


Figure 28. Interspecific dendrogram of three domestic *Panicum* species by AFLP markers

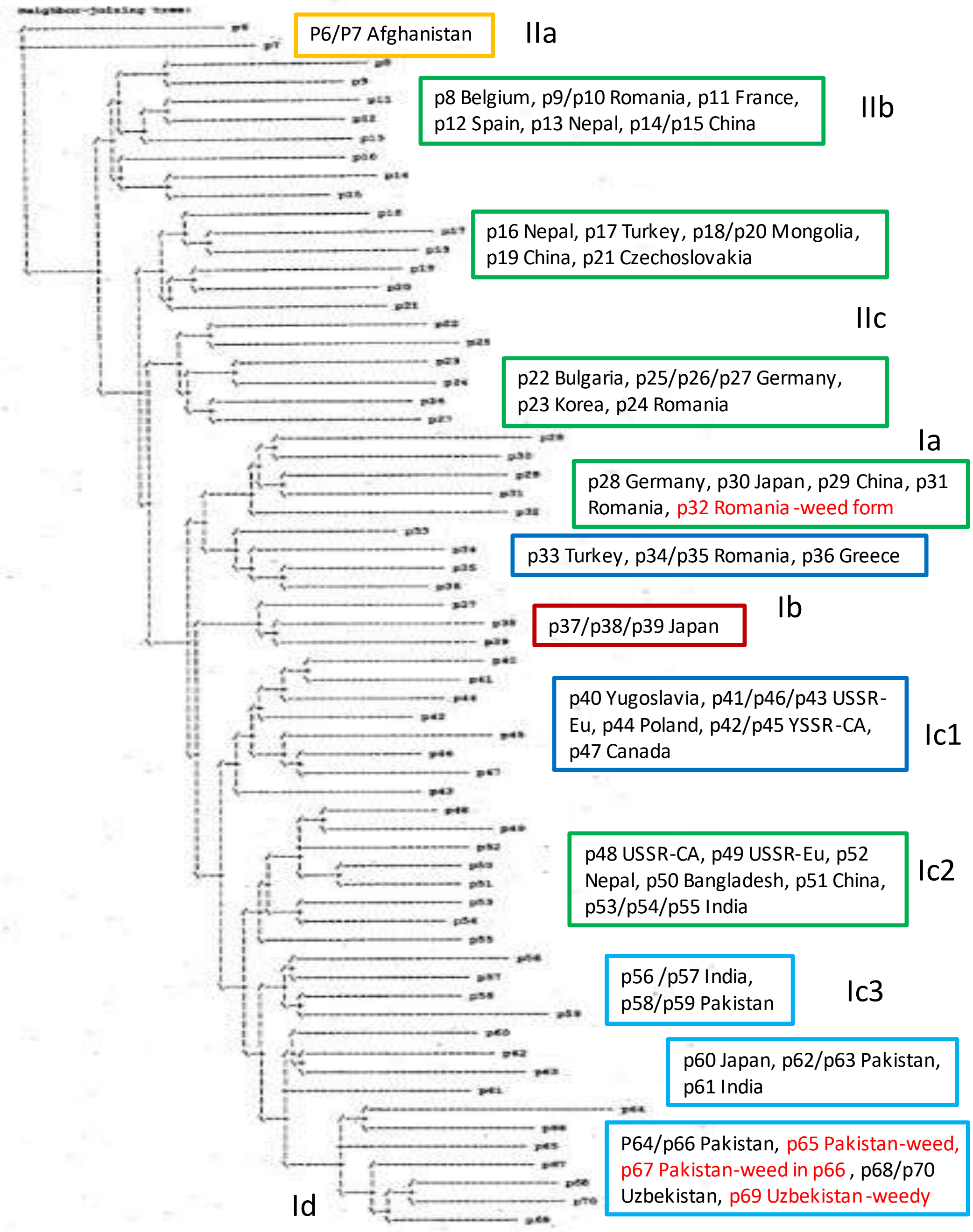


Figure 29. Intraspecific dendrogram of common millet by AFLP markers.

Food preparation and secondary compounds in grain

Eurasian dishes made from common millet are classified into four processing methods: grain, coarse-ground flour, fine flour, and beverages. In Asia, people use polished grains of non-glutinous varieties to cook boiled grain dishes and porridge (Table 20 and 21). East Asians, in particular, prepare steamed grain and *mochi* (a type of cake) with polished grains from glutinous varieties. Both non-glutinous and glutinous polished grains are used for fermenting alcoholic drinks. Inner Mongolians regularly drink daily milk tea prepared with roasted grains (Figure. 30a), while Uzbeks garnish non (bread) with colored grains (Figure 30b) and serve milk porridge made from non-glutinous varieties at nursery schools for lunch (Figure 30c). In Europe, milk porridge is prepared from coarse-ground flour, bread from fine flour, and only non-glutinous polished grains are used to ferment non-alcoholic drinks.

Millet seed grain varieties are categorized as either glutinous or non-glutinous based on endosperm starch types. The glutinous varieties of common millet and *Setaria italica* are primarily found in eastern Asia. The geographical distribution of phenol color reactions in the seed coats of *S. italica* closely resembles that of *O. sativa*, but differs from common millet which resembles the trends of *S. italica* and *O. sativa* (Sakamoto 1982, Kawase and Sakamoto 1982, Kimata and Negishi 2002).

Table 20. Iodo-starch reactions of endosperms (waxy and non-waxy)

Locality	No. of strains	Color reaction: No. of strains (%)			
		Red-brown (waxy)	Grape (medium)	Blue (non-waxy)	Undicided
Japan	132				
Hokkaido	16	1 (6.3)	15 (93.7)	0	0
Honshu	57	33 (57.9)	21 (36.8)	3 (5.8)	0
Sikoku	30	23 (76.7)	7 (23.3)	0	0
Kyushu	9	6 (66.7)	3 (3.3)	0	0
South West islands	20	13 (68.4)	6 (31.6)	0	1
East Asia	39				
Korea	23	11 (50.0)	5 (22.7)	6(27.3)	1
China	10	6 (60.0)	1 (10.0)	3 (30.3)	0
Mongolia	6	0	0	6 (100)	0
South Asia	90	0	0	90 (100)	0
West Asia	26	0	1 (3.8)	25 (96.2)	0
Former Soviet Union	78				
Central Asia	12	0	0	12 (100)	0
Others	66	1 (1.5)	2 (3.0)	63 (95.5)	0
Europe	43	0	1 (2.4)	41 (97.6)	1
Africa	2	0	0	2	0
North America	1	0	0	1	0
Total	411	94 (23.0)	62 (15.2)	252 (61.8)	3

Modified by Kimata & Negishhi (2002)

The four types of local common millet varieties were classified by the presence of minor fatty acids (arachidic, behenic, eicosapentaenoic acid). The ancestral prototype was the weedy AE type containing arachidic and eicosapentaenoic acids; the AB type (arachidic and behenic acid) likely developed in Europe and Asia, while ABE (all three fatty acids) and O (no fatty acids) types may have originated near Central Asia before spreading to Europe and Asia (Kimata et al. 2007).

Table 21. Foods made from common millet around Eurasia

Locality	glutinous/non-glutinous	grain				coarse-ground flour	ground flour			drinks	
		boiled	steamed	porridge	*mochi*	porridge	dumpling	gruel	bread	non-alcohol	alcohol
Japan	non-glutinous	○		○			○	○			
	glutinous		○		○		○				○
Korea	non-glutinous	○									
	glutinous		○		○						○
China	non-glutinous	○		○					○		○
	glutinous		○		○				○		○
Taiwan	non-glutinous	○									
	glutinous		○		○		○				○
Bataan Isles	non-glutinous					○					
Halmahera	non-glutinous					○					
India	non-glutinous	○				○		○	○		
Pakistan	non-glutinous	○							○		
Afghanistan	non-glutinous					○	○		○		
Uzbekistan	non-glutinous					○			○		
Kazakhstan	non-glutinous					○					
Caucasia	non-glutinous					○				○	
Turkey	non-glutinous					○					
Ukraine	non-glutinous					○				○	
Bulgaria	non-glutinous					○				○	
Romania	non-glutinous					○			○		
Germany	non-glutinous					○					
Belgium	non-glutinous					○					
Italy	non-glutinous					○					

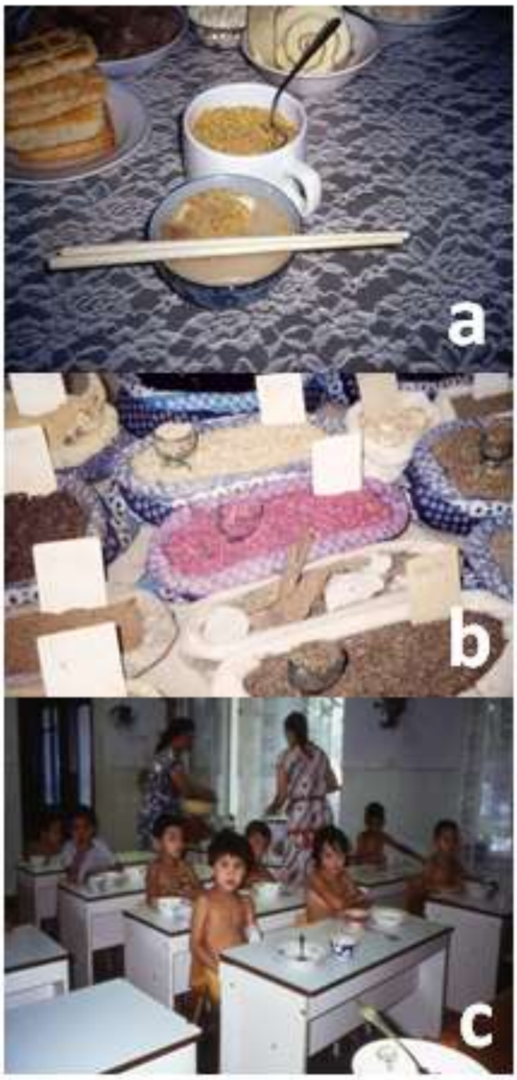


Figure 30. Foods made from common millet in Uzbekistan and Inner Mongolia.
a, Milk tea with roasted grains in Inner Mongolia; b, colored grains as a topping for bread in Uzbekistan; c, milk porridge for lunch at a nursery school in Uzbekistan.

Vernacular names of *P. miliaceum*

The word for "common millet" typically uses prefixes such as "*ki-*," "*che-*," "*va-*," or "*ba-*" in East and South Asia, while several variations exist in China (Table 22). In Central Asia and the mountainous area of Pakistan, the prefixes are diverse. Western Asia and Egypt mainly use the prefix "*d-,*" while in Europe, prefixes like "*mi-*" and "*proso*" are common. The diversity of vernacular names for common millet throughout Eurasia indicates that this crop has been domesticated or broadly dispersed from a very early period.

In the Indian subcontinent, common millet is known as "*cheena*," "*chiena*," or "*chin.*" Based on the Farming/Language Dispersal Hypothesis (Bellwood and Renfrew 2002), these vernacular names might be derived from China and the term "Qin" (an ancient Chinese Empire), suggesting a dispersal route from China to the Indian subcontinent through Nepal.

Table 22. Vernacular names of *P. miliaceum* around Eurasia

Region	Country	Modern name	Ancient name
East Asia			
	China	chi, huangmi, nianmi, shu, shuzi,	shu
	Inner Mongolia	horei bata	
	Korea	kijan	
	Japan	inakibi, kibi, kokibi	kimi, shipshi-kepp
Central Asia			
	Kazakhstan	psheno	
	Afghanistan	arzan	
South Asia			
	Pakistan		
	North	bau, cheena, chiena, olean, onu	
	South	tzetze	
	India		
	North	charai, cheena, chin, china, sawan, worga	unoo, vreelib-heda, vreehib-heda
	South	baragu, cheena, , katacuny, pani baragu, tane, variga, varagu, wari	
	Nepal	china	
	Sri Lanka	mene'ri	
West Asia			
	Arabia	dokhn, kosaejb, kosjaejb	
	Turkey	dari, kundari	
	Israel	dokhan	
Africa			
	Egypt	dokhn	
Europe			
	Greece		kegchros
	Hungary	ko˝les	
	Russia	proso	
	Poland	proso	
	Croatia	proso	
	Lithuania		sora
	Netherlands	gierst	
	Germany	rispen hirse	
	Italy	milium	miglio
	Spain	mijo commun	
	France	millet commun	
	United Kingdom	common millet	mill

cf. Kawase 1991, Sakamoto 1986, and many dictionaries.

Domestication process and dispersal of common millet

The origins, domestication, and geographical dispersal of common millet have been explored by synthesizing findings from various archaeological studies (e.g., Fuller et al. 2001, Hunt and Jones 2006, Jones 2004, Nesbitt 2005). A current hypothesis, supported by genetic diversity and crossbreeding records across Eurasia, suggests that common millet's domestication began in Central Asia (Figure 31); however, more research is needed on the crop's evolutionary relationships.

From its Central Asia origin, common millet gradually spread to China, then moved southward into South Asai, directly west into Europe, and indirectly to southeastern Europe via West Asia. Additionally, common millet might have dispersed from China to Japan and Southeast Asia. While Near Eastern farmers who grew barley and wheat did not always adopt common millet, nomadic groups traversing the Eurasian steppes readily accepted it as a food source due to its rapid growth during short summers and as valuable animal fodder—similar to how Mongolian herdsmen use it today. These nomads played a significant role is spreading millet eastward and westward from

Central Asia. Common millet might have dispersed more rapidly along east–west lines at similar latitudes than it did north–south across varying climates, maturing quickly in summer when barley and wheat remained slow-growing.

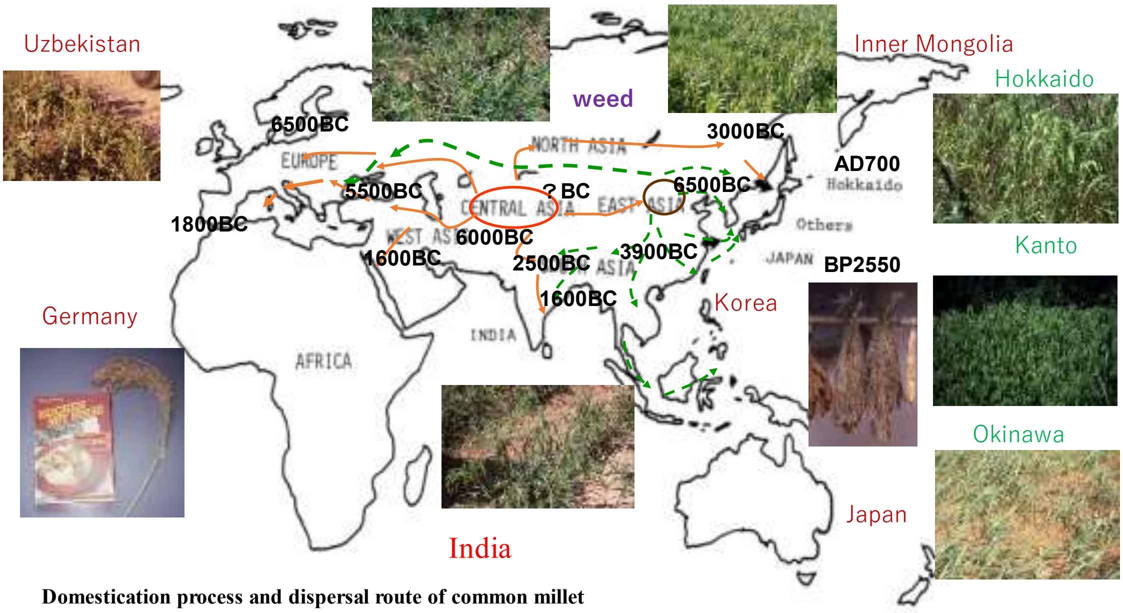
Traditional varieties cultivated by the Ainu people in Hokkaido, Japan, closely resemble those from North China and Mongolia in their panicle type and the duration to flowering, while the other Japanese varieties are similar to those from Korea and Nepal in their panicle type and stigma color (Kimata et al. 1986). High variation in grain and panicle characteristics is also observed among former USSR and European varieties. Notably, Indian and West Asian varieties show extensive diversity in many characteristics.

Compared with other Eurasian varieties, those from Afghanistan, Pakistan, India, and Central Asia exhibit particularly broad diversity, including sparse panicles and numerous tillers. Mapping the geographical distribution of these traits provides useful information regarding biocultural diversity, including traditional foods and local names, which help reconstruct the domestication process and dispersal routes (Kimata 2015c).

Ancestral forms of common millet might have matured early, shattered easily, produced smaller grains and more tillers, had pale brown lemmas, white stigmas, glabrous uppermost internodes, and non-glutinous starch. In contrast to domesticated cereals—with typically fewer tillers—many Central and South Asian varieties retain ancestral characteristics. Although there is a relative dearth of data on the mimic weed type associated with domesticated forms (Sakamoto 1988, Scholz and Mikolāš 1991), several weed types with remarkable grain shattering have been documented in Pakistan, Uzbekistan, and Kazakhstan (Kimata 1994, 1997). Due to the ongoing presence of wild relatives and their variability, Central Asia show is strongly indicated as common millet's primary domestication center. Moreover, the weed types were classified into two subspecies, *ruderale* and *agricolum*, and a crop-like weedy biotype escaped from the domestic type. It seems that *ruderale* was an ancestor, while *agricolum* became a weed by hybridization between these two subspecies.

Common millet was first domesticated from wild *P. miliaceum* subsp. *ruderale* in Central Asia, including the northern mountains of Afghanistan and Pakistan, especially near the Aral Sea and the Southwest Tien Shan Mountains. It later dispersed in all directions: east to China, west to Europe, south to the Indian subcontinent (de Wet 1995), and north to Siberia, largely through nomadic movements since the Neolithic era. Historical accounts indicate that the Mongolian army introduced common millet to Europe during the thirteenth century invasions (Carpine 1246). Morphological and genetic analyses indicate that certain Chinese varieties cluster with European varieties, supporting evidence for this transmission route (Figures 3 and 5). Additionally, the traditional varieties cultivated by the Ainu people in Japan (Hokkaido) are similar to those from North China and Mongolia in their panicle type and early duration to flowering, while other Japanese varieties resemble those from Korea and Nepal in their panicle type, stigma color, and phenol reaction of young lemmas (Kimata et al. 1986, Kimata and Negishi 2002). A northern route from North China into Hokkaido is further supported by the fact that PC57-2 (Hokkaido, Japan) generated fertile hybrids among the testers from Central Asia, India, and Japan.

Common millet (*Panicum miliaceum* L.) was once the primary crop throughout Eurasian civilization for thousands of years beginning in the Neolithic era. Today, it remains widely cultivated and used across the world. Despite its ancient history as one of Eurasia's earliest domesticated plants, researchers have yet to definitively identify its ancestral species or precise place of origin. To better understand how common millet was domesticated and dispersed, a series of investigations involving the plant’s morphology, ecology, genetics, and secondary compounds were performed. These studies utilized 650 local varieties collected from local famers and additional herbarium specimens to assess physical characteristics, crossability, DNA markers, phenol and iodine color reactions, seed fatty acid profiles, traditional food preparations, and archeolinguistic data. By combining these findings, researchers concluded that common millet was domesticated with a wild population of *P. miliaceum* subsp. *ruderale* in Central Asia, specifically in the region stretching from the Aral Sea to the Southwest Tien Shan Mountains. Since the Neolithic era, nomadic groups have spread the millet east to China, west to Europe, south to the Indian subcontinent, and north to Siberia.



Domestication process and dispersal route of common millet based on the botanical data and archaeological excavation

Figure 31. Dispersal routes of common millet through the Eurasia

Chapter 5 Domestication Process of Millets in the Indian Subcontinent

The Indian subcontinent is among the most interesting and significant regions for millet research. For centuries, numerous farmers have cultivated many types of millet species, and the grains have served as a staple food for many people since ancient times. This subcontinent is uniquely positioned to contribute to our understanding of the domestication process of millets due to its rich agricultural heritage and diversity. Despite this, researchers in anthropology and ethnology have traditionally shown limited interest in the millets domesticated within the Indian subcontinent, leaving a gap in the comprehensive study of these important crops.

A pioneering researcher in this field, Kobayashi, H., made significant advances in the study of secondary crop domestication. Sadly, his work was cut short when he contracted malaria during a research expedition in Africa and passed away in 1994. In honor of his legacy and as a tribute to a close friend with whom many journeys to India were shared, I took up the responsibility of continuing his research.

Another essential contributor to the collaborative research effort was Seetharam, A., a skilled coordinator who lent invaluable support to the millet studies conducted across the Indian subcontinent. His passing in 2025 is felt by all who benefited from his kindness and expertise.

Field research expeditions in the Indian subcontinent

Over the years, I have participated in six major field expeditions for millet research. These expeditions yielded a substantial collection of millet accessions and their related species, as well as detailed information regarding their agricultural complexes. The data were gathered directly from hundreds of farmers in their villages and fields, ensuring authentic and comprehensive documentation (Table 23).

The expeditions primarily focused on the southern foothills of the Himalayas and the Western and Eastern Ghats, extending across the Indian subcontinent between 1983 and 2001. The reach these diverse and often remote regions, the research teams relied on many transportation methods, including cars, trains, airplanes, and travel by foot (Figure 31). The field trips covered a wide geographic range, encompassing Karnataka, Andhra Pradesh, Tamil Nadu, Maharashtra, Telangana, Maharashtra, Madhya Pradesh, Orissa, Chhattisgarh, Jharkhand, West Bengal, Bihar, Uttar Pradesh, Uttarakhand, Himachal Pradesh, and Jammu and Kashmir in India, as well as the North–West Frontier in Pakistan and Eastern Nepal.

Table 23. Millet research expeditions across the Indian subcontinent from 1983 to 2001

Year (month)	Locality	Research Team
1983.9-11	Nepal, India (Hariana)	The Japanese Scientific Expedition for Nepalese Agricultural Research
1985.9-11	Pakistan (Northwest province), India (Karnataka, Andhra Pradesh, and Tami Nadu)	Kyoto University Scientific Expedition to the Indian Subcontinent
1987.9-11	India (Jammu and Kashmir, West Bengal, Orissa, and Assam), Pakistan (Sind)	Kyoto University Scientific Expedition to the Indian Subcontinent
1989.9-10	Pakistan (Azad Kashmir), India (Karnataka, Madhya Pradesh, and Maharashtra)	Kyoto University Scientific Expedition to the Indian Subcontinent
1996.9～97.6	India (Karnataka, Andhra Pradesh, Tamil Nadu, Orissa, Himachal Pradesh, and Utter Pradesh)	Research abroad supported by Japanese Government, University of Agricultural Sciences at Bangalore
2001.9-10	India (Karnataka and Orissa)	Tokyo Gakugei University Scientific Expedition to the Indian Subcontinent

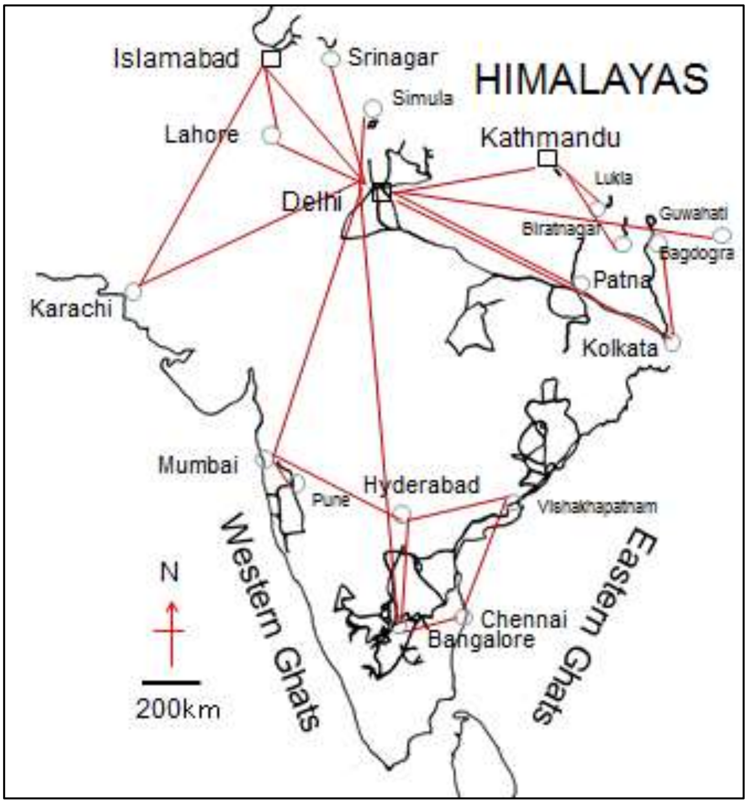


Figure 31. Expedition routes in the Himalayas, Western Ghats, and Eastern Ghats.

Grain crops grown in the Indian subcontinent

The Indian subcontinent presents valuable opportunities for investigating the domestication of grain crops (Table 24). This region has served as a center for the domestication of several millet species. Grain crops grown within this subcontinent are classified into four main groups according to their geographical origin: (I) African origin: *Eleusine coracana* (L.) Gaertn., *Pennisetum glaucum* (L.) R. Br., and *Sorghum bicolor* Moench; (II) Mediterranean origin: *Hordeum vulgare* L. and *Triticum* spp.; (III) Asian origin, comprising four subgroups—(a) *Panicum miliaceum* L. and *Setaria italica* (L.) P. Beauv.; (b) *Coix lacryma-jobi* L. var. *ma-yuen* (Roman.) Stapf. and *Oryza sativa* L.; (c) *Echinochloa frumentacea* (Roxb.) Link, *Panicum sumatrense* Poth., *Paspalum scrobiculatum* L., *Digitaria cruciata* (Nees) A. Camus., *Setaria pumila* (Poir.) Roem. & Schult, and *Brachiaria ramosa* (L.) Stapf.; and (d) Southwestern China, *Fagopyrum esculentum* Moench, *Fagopyrum tataricum* (L.) Gaertn.—and (IV) New World: *Zea mays* L., including *Amaranthus hypocondriacus* L., *Amaranthus caudatus* L., and *Chenopodium quinoa* Willd. These groups and the associated agricultural complexes have been introduced to the Indian subcontinent multiple times throughout prehistoric and historic periods.

Many millet species continue to be cultivated by farmers across the subcontinent. These species are organized into three groups based on their place of origin: (1) Asia, including the indigenous Indian subcontinent, Central Asia, Southeast Asia, and Tibet; (2) Africa; and (3) the New World. Seven Asian millet species, including *Panicum miliaceum*, *Setaria italica*, *Coix lacryma-jobi* var. *ma-yuen*, *Fagophyrum esculentum*, and *Fagophyrum tartaricum,* originated from Central Asia, Southeast Asia, and Tibet. The African species—*Eleusin. coracana*, *Sorghum bicolor*, and *Pennisetum glaucum*—were introduced via the Arabian peninsula around 2000 BC (Sakamoto 1987, Ohnishi 1998). The New World pseudocereals—*Amaranthus caudatus*, *Amaranthus hypocondriacus*, and *Chenopodum quinoa*—were introduced in 19th century (Sauer 1976).

Table 24. Grain crops grown in the Indian subcontinent

Geographical origin Scientific name	Japanese name	Indian name	Chromosome number	Growth habit	Botanical origin
Africa					
Sorghum bicolor	morokoshi	jowar	2n=20 (2x)	annual	*S. bicolor* var. *verticilliflorum*
Pennisetum americanum	toujinn-bie	bajra	2n=14 (2x)	annual	*P. violaceum*
Eleusine coracana	shikoku-bie	ragi	2n=36 (4x)	annual	*E. coracana* var. *africana*
Asia					
1. India					
Panicum sumatrense		samai	2n=36 (4x)	annual	*P. sumatrense* ssp. *psilopodium*
Paspalum scrobiculatum		kodo	2n=40 (4x)	perennial	wild
Echinochloa flumentacea	indo-bie	jangora	2n=54 (6x)	annual	*E. colona*
Brachiaria ramosa		korne		annual	wild
Setaria pumila	kin-enokoro	kolati		annual	wild
Digitaria crusiata		raishan		annual	wild
2. South-eastern Asia					
Coix lacryma-jobi var. *ma-yuen*	hatomugi		2n=20 (2x)	perennial	*C. lacryma-jobi* var. *lacryma-jobi*
3. Central Asia					
Setaria italica	awa	thenai	2n=18 (2x)	annual	*S. italica* ssp. *viridis*
Panicum miliaceum	kibi	cheena	2n=36 (4x)	annual	*P. milliaceum* ssp. *ruderale*
4. South-western Asia					
Fagopyrum esculentum	soba		2n=16 (2x)	annual	*Fagopyrum esculentum* ssp. *ancestralis*
Fagopyrum tartaricum	dattan-soba		2n=16 (2x)	annual	*Fagopyrum tartaricum* ssp. *potanini*
New world					
Amaranthus hypocondriacus	sen-ninkoku		2n=32, 34 (2x)	annual	*A. cruentus (A. hybridus)*
Amaranthus caudatus	himogeitou		2n=32, 34 (2x)	annual	*A. cruentus (A. hybridus)*
Chenopodium quinoa	kinoa		2n=36 (4x)	annual	*C. quinoa* ssp. *milleanum*

Indigenous millet species have been domesticated in the Indian subcontinent for approximately 3,500 years (Fuller 2002). The species include *Echinochloa furumentacea*, *Panicum sumatrense*, *Paspalum scrobiculatum*, *Brachiaria ramosa*, *Setaria pumila*, *Digitaria cruciata*, and *Digitaria sanguinalis*. Of these, the first three are thought to have originated as secondary crops, evolving from mimic or companion weeds alongside rain-fed paddy and upland rice in Eastern India. *Brachiaria ramosa* and *Setaria pumila* also became secondary crops through their association with other millet species via their mimic/companion weed types in Southern India. *Digitaria cruciata* was domesticated in the late 19th century by Kashi natives in Meghalaya, where it is still grown in the Kashi Hills (Singh and Arora 1972). In contrast, *Digitaria sanguinalis* has disappeared and its origin remains uncertain.

The domestication of millets is always accompanied by a basic agricultural complex, comprising cultivation techniques, processing, cooking methods, religious uses, vernacular nomenclature, and other aspects. Millet's center of domestication includes the Eastern Ghats and Southern Deccan Plateau, determined through field studies, experimental results, linguistic research, and archaeological data. Although this process is complex, understanding its development as an insurance crop, mimic companion weed, or weed type offers valuable insights. This process highlights the significance of the weed–crop relationship and broader agricultural complexes as examples of plant–man symbiosis. Additionally, many words in old Indo-Aryan and Dravidian languages relate directly to millet names. Hence, *Brachiaria ramosa* and *Setaria pumila* are considered "tertiary crops,"—double-secondary crops for other millets and upland rice. Historical site findings typically support this sequence of millet evolution.

Ancient farmers domesticated six millet species from related weed species in India, after which these plants spread across the subcontinent and neighboring areas.

Panicum sumatrense (*samai*) is an annual tetraploid (2n = 36) derived from *Panicum sumatrense* ssp. *psilopodium* (Figure 32a). *Paspalum scurobiculatum* (*kodo*) is a perennial tetraploid (2n = 40, Figure 32b), while *Echinochloa furumentacea* (*jangora*) is an annual hexaploid (2n = 54, Figure 33c) derived from the relative weed *Echinochloa colona*. *Brachiaria ramosa* (*korne*) and *Setaria pumila* (*kolati*) are annual (Figure 32d and 32e), secondary crops domesticated from their relative weeds in paddy fields. *Digitaria cruciata* (*raishan*) is an annual plant derived from weeds growing among maize and vegetables (Singh and Arora 1972). Additionally, *Oryza rufipogon* Griff. (wild rice) is used as an offering to gods and goddesses during festivals and grows in ponds and irrigation canals near paddy fields (Figure 32f).

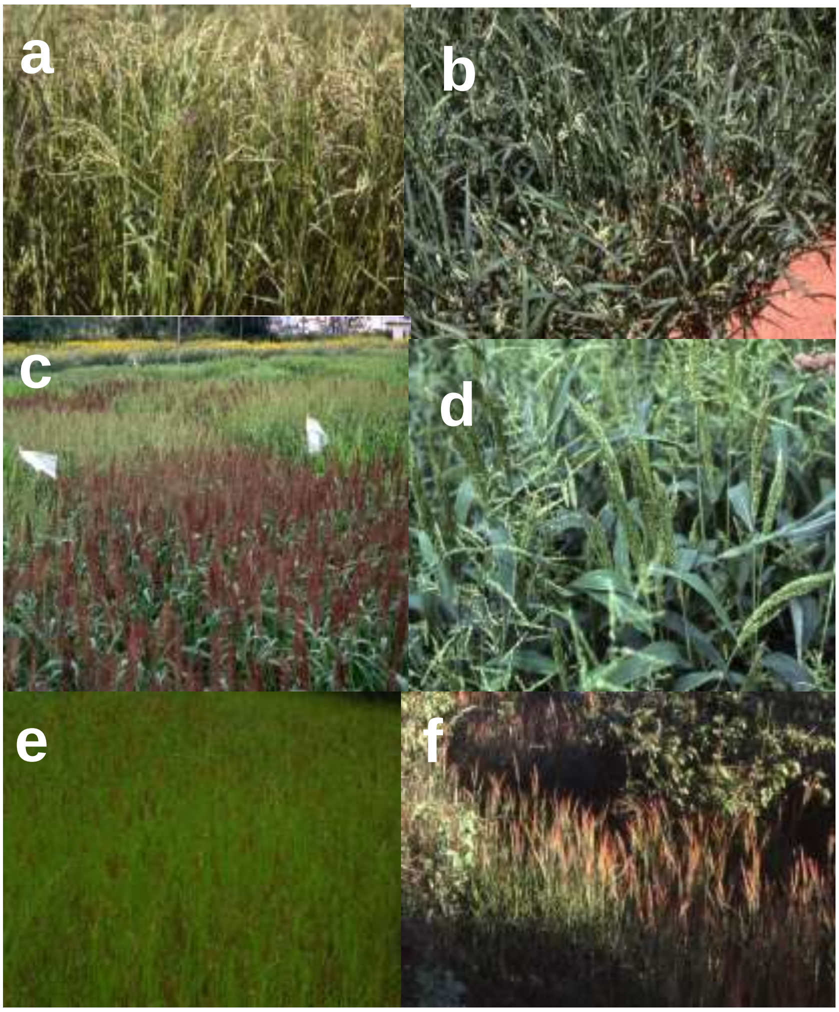


Figure 32. Five species of millet and wild rice domesticated in the Indian subcontinent:
a, *Panicum sumatrense*; b, *Paspalum scrobiculatum*; c, *Echinochloa frumentacea*; d, *Brachiaria ramosa*; e, *Setaria pumila*; and f, *Oryza rufipogon* in the irrigation canal.

During the era of the Indus Civilization, or prior to recorded history, Indian farmers introduced six millet species from Africa via multiple routes: the Arabian Peninsula, Central Asia through the Himalayas, and Southeast Asia via Assam. *Sorghum bicolor* (*jowar*) is an annual, diploid species (2n = 20, Figure 33a) originating from *Sorghum bicolor* var. *verticilliflorum* in Eastern Africa. *Pennisetum glaucum* (*bajra*) is an annual, diploid plant (2n = 14, Figure 33b), domesticated from *Pennisetum violaceum* in Africa. *Eleusine coracana* (*ragi*) is an annual, tetraploid plant (2n = 36, Figure 33c) domesticated from *Eleusine coracana* var. *africana* in Eastern Africa.

Setaria italica (*thenai*) is an annual, diploid plant (2n = 18, Figure 33d) that originated from *Setaria viridis*, a cosmopolitan weed in Central Asia. *Panicum miliaceum* (*cheena*) is an annual, tetraploid species (2n = 36, Figure 33e), domesticated from *Panicum miliaceum* ssp. *ruderale* in Central Asia. *Coix lacryma-jobi* var. *ma-yuen* is a perennial, diploid species (2n = 20), domesticated from *Coix lacryma-jobi* var. *lacryma-jobi* in Southeast Asia. These millet species are predominantly cultivated using mixed or intercropping systems(Anders et al. 1996). For instance, *Setaria italica* is often grown and mixed with *Glycine max* (Leguminosae; Figure 33f).

Moreover, five pseudocereal species are cultivated in the Indian subcontinent. *Fagophylum esculentum* and *Fagophylum tartaricum* (both annual, 2n = 16, diploid) were introduced from Tibet. More recently, *Amaranthus caudatus*, *Amaranthus hypocondriacus* (both annual, 2n = 32 or 34, diploid), and *Chenopodeum quinoa* (annual, 2n = 36, tetraploid) have been introduced from the New World.

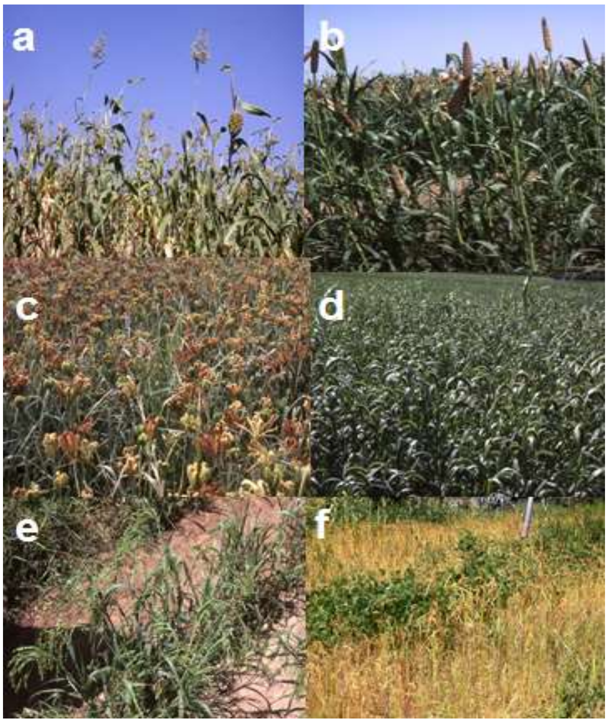


Figure 33. Five species of millet introduced into the Indian subcontinent and an inter-cropping field with *Setaria italica* and *Grycine max*:

a, *Sorghum bicolor*; b, *Pennisetum glaucum*; c, *Eleusine coracana*; d, *Setaria italica*; e, *Panicum miliaceum*; and f, inter-cropping field.

This special issue on Indian millets presents research focused on the agricultural complex, domestication process, and millet dispersal, with particular emphasis on *Setaria pumila* (syn. *S. glauca*) and *P. milliaceum,* rather than on major crops such as rice, wheat, barely, and maize. *S. pumila* is now found only in a confined area of the Deccan Plateau (Kimata 2015a, 2015b), while *P. milliaceum* has been dispersed throughout Eurasia (Kimata 2015d), including the Indian subcontinent, and has recently spread to North America and Australia. These contrasting distribution patterns offer intriguing insights from an environmental history and geography perspective, highlighting the remarkable differences in the spread of *S. pumila* and *P. milliaceum*.

Morphological characteristics of *Setaria pumila*

Statistical analyses of partial correlation coefficients were conducted for ten morphological characteristics of *S. pumila:* number of tillers, plant height, spike length (pl), spike width (pw), the ratio of pl/pw, flag leaf length (fll) and width (flw), the fll/flw ratio, last internode diameter, and duration to flowering (Table 25). These traits are strongly influenced by artificial selection during the domestication process. Seed size and seed shattering served as the controlled variables

Significant statistical correlations were observed at the 1% level for various trait combinations: fll/flw ratio to plant height (-0.517); pl/pw ratio (0.739), fll (0.664), flw (0.584), and last internode diameter (0.716) to pl; pl (0.739) and ffl (0.704) to the pl/pw ratio; pl (0.664), pl/pw ratio (0.704), ffl/ffw ratio (0.720), and duration to flowering (-0.544) to fll; pl (0.584), fll/flw ratio (-0.508), and last internode diameter (0.882) to flw; plant height (-0.517), fll (0.720), flw (-0.508), and duration to flowering (-0.561) to the fll/flw ratio; spike length (0.716) and flw (0.882) to the last internode diameter; and fll (-0.544) and fll/flw ratio (-0.561) to the duration to flowering. No significant correlations were found between the number of tillers and the last internode diameter ($p < 0.01$).

Table 25. Partial correlation coefficients of morphological characteristics in *Setaria pumila*

characteristics	tillers	plant height	spike length	spike width	sl/sw	flag leaf length	flag leaf width	fll/flw	first node diameter	dulation to flowering
tillers	1	−0.142	−0.055	−0.410*	0.221	0.166	−0.289	0.301	−0.239	−0.095
plant height	−0.142	1	0.256	−0.001	0.086	−0.224	0.404*	−0.517**	0.388*	0.211
spike length	−0.055	0.256	1	0.151	0.739**	0.664**	0.584**	0.166	0.716**	−0.242
spike width	−0.410*	−0.001	0.151	1	−0.455*	−0.132	0.254	−0.251	0.227	−0.091
sl/sw	0.221	0.086	0.739**	−0.455*	1	0.704**	0.172	0.488*	0.292	−0.227
flag leaf length	0.166	−0.224	0.664**	−0.132	0.704**	1	0.194	0.720**	0.311	−0.544**
flag leaf width	−0.289	0.404*	0.584**	0.254	0.172	0.194	1	−0.508**	0.882**	0.122
fll/flw	0.301	−0.517**	0.166	−0.251	0.488*	0.720**	−0.508**	1	−0.35	−0.561**
first node diameter	−0.239	0.388*	0.716**	0.227	0.292	0.311	0.882**	−0.35	1	0.171
dulation to flowering	−0.095	0.211	−0.242	−0.091	−0.227	−0.544**	0.122	−0.561**	0.171	1

Control variables: grain size、shattering

Cluster analysis of six morphological characteristics (number of tillers, plant height, sl, fll, flw, and fll/flw ratio) and the duration to flowering (Figure 33). Using the Ward method, 60 accessions were categorized into three clusters and several sub-clusters. Cluster I comprised sub-clusters Ia and Ib; Ia (7 accessions) included the weed type (W2), companion weed types (Ws1) from Maharashtra, companion weed type (Ws1), mimic companion weed type (medium, Ms2), and domestication type mixed with *samai* (*P. sumatrense*, Ds1) from Orissa. Ib (5 accessions) included Ds5 from Andhra Pradesh (3), Karnataka (1), and Maharashtra (1). Cluster II contained sub-clusters IIa and IIb; IIa (17 accessions) included Ds1, Ms2, Mk4, Ws3, and W3 from Orissa, Dk2 from Karnataka, and Ws2 from Maharashtra; IIb (2 accessions) included Ms1 and Ws1 from Orissa. Cluster III comprised sub-clusters IIIa–c; IIIa (1 accession) contained W1 from Maharashtra; IIIb (10 accessions) included Mk1, Ws6, Wk1, and W2 from Orissa; IIIc (11 accessions) included Ds1, Dk1, Ms1, Mk2, Mp3, Ws1, and W1 from Orissa, and W1 from Maharashtra. The "W" type of *S. pumila* was distributed across the Indian Subcontinent as a cosmopolitan weed.

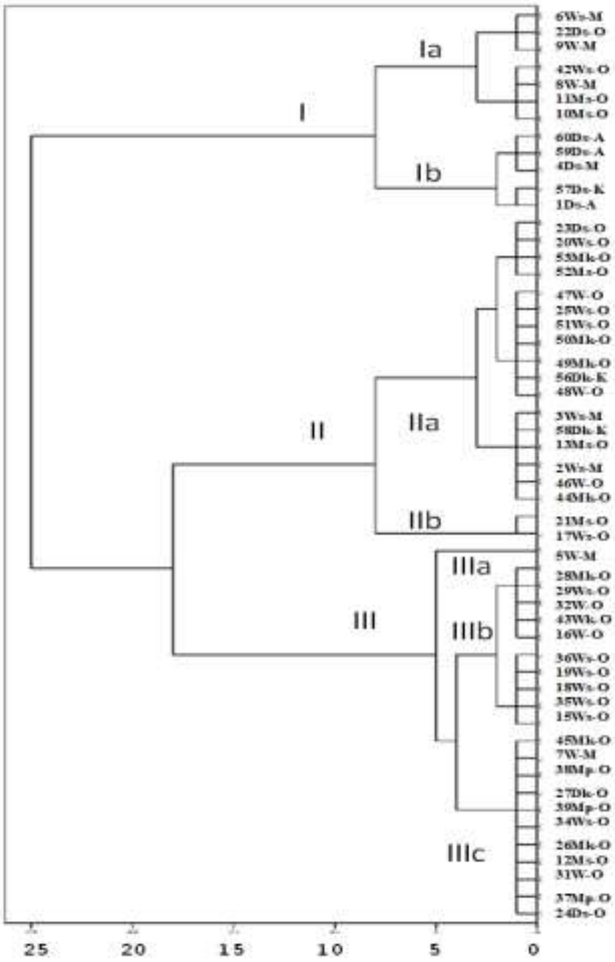


Figure 33. Cluster analysis of six morphological characteristics

Species component of millet and weed grown in four cropping fields (investigation sites)

The annual species composition ratios within each mixed cropping field exhibited variability, influenced by environmental factors such as summer precipitation. During the early growth stages, morphological differentiation among the various plant species collected from the same cropping field was often challenging. Both inter- and intra-specific mimicry manifested not only in morphological characteristics—such as plant height, leaf size, and tiller number—but also in ecological traits, including seed germination patterns, seed color, and leaf sheath color. Notably, the leaf sheath color of *P. sumatrense* and *Pas. scrobiculatum* (Sub-cluster IIa) was found to mimic that of *S. pumila* (Cluster I), while the glume color of *S. pumila* exhibited mimicry of *P. sumatrense*. It appears that the domestication and dispersal of *S. pumila* have occurred through elaborate mimicry of several key crop characteristics.

Table 26 presents the species composition (per m²) across four millet cultivation fields. At site 1, the proportions of *P. sumatrense*, *S. pumila,* and the weed *Brachiaria* sp. were 59%, 33%, and 8%, respectively. Conversely, at site 2, the proportion shifted to 25%, 74%, and a trace amount. Site 3 consisted of a single stand of *E. coracana*, while site 4 was a monoculture of *P. sumatrense*; however, the weedy form of *S. pumila* had invaded both fields, accounting for only 3–5% of the populations in each cropping field.

Table 26. Component species per m^2 of investigation sites

Site no.	Locality	*Panicum sumatrense*	*Setaria pumila*	*Eleusine coracana*	*Brachiaria* sp.	*Digitaria* sp.	Total
Site 1	**01-10-8-2 (805m alt.) Cittoor, Andhra Pradesh**						
	No. of plants	163.5	90.75	0	22	0.25	276.5
	s.d.	76.43	36.48		24.99	0.5	75.54
	Range	78-264	55-141		0-56	0-1	191-355
	%	59.13	32.82	0	7.96	0.09	100
	Highest plant (cm)	77.38	66.88				
	s.d.	7.63	10.17				
Site 2	**01-10-9-1 (690m alt.), Cittoor, Andhra Pradesh**						
	No. of plants	105.5	312.25	0	0.75	1	419.5
	s.d.	68.83	60.91		0.5	0.82	68.98
	Range	30-172	240-368		0-1	0-2	352-517
	%	25.15	74.43	0	0.18	0.24	100
	Highest plant (cm)	76	68.25				
	s.d.	24.07	15.37				
Site 3	**01-10-17-1 (855m alt.) Kundli, Orissa**						
	No. of plants	1.75	1.5	42.25	0	0.25	45.75
	s.d.	0.96	1	6.85		0.5	26.12
	Range	1-3	1-3	34-50		0-1	46-101
	%	3.83	3.28	92.35	0	0.55	100
Site 4	**01-10-19-3 (375m alt.), West Polehorebrdle, Orissa**						
	No. of plants	40.5	2	0	0	0	45.75
	s.d.	8.23	1.63				20.59
	Range	30-50	0-4				40-86
	%	95.29	4.71	0	0	0	100

Domestication process of *Setaria pumila*

The domestication of *S. pumila* may have passed through four distinct stages (Figure 34). The initial phase began with a weed, thriving along roadsides and other unstable habitats. Over time, these weeds invaded upland rice fields.

The second phase involved an evolutionary shift beyond its status as a simple weed to occupy an agro-ecological niche. During this period, it was utilized as fodder, which facilitated its recognition as a companion weed in upland rice and certain millet fields.

The third phase saw the advancement from a mimic companion weed to a semi-domesticated insurance crop, used in case of famine, under mixed cropping with *Pas. scrobiculatum*, *E. coracana*, and *P. sumatrense*. Through its invasion into upland rice and millet fields, certain weed types developed mimicry associated with particular crops, resulting in a closely integrated weed–crop complex. This relationship was reinforced by the rigorous weed control measures employed by farmers.

In the fourth and final phase, the mimic companion weed forms of *S. pumila* were used as fodder for cattle and as a supplementary grain to the main cereal species.

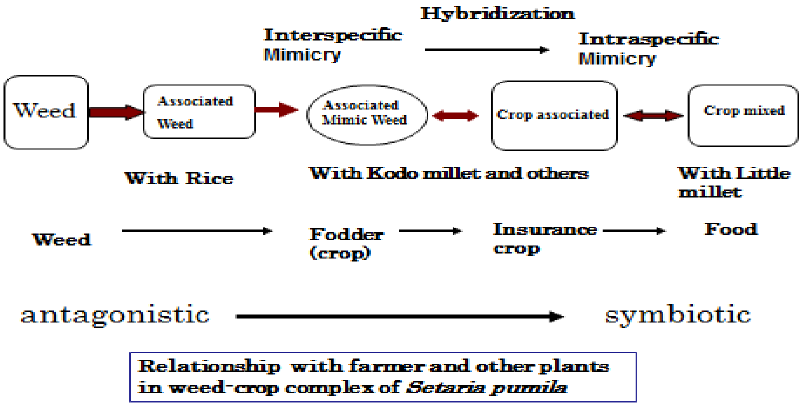


Figure 34. Domestication process of *Setaria pumila*

Within the context of *S. pumila*, farmers in the Deccan Plateau deliberately avoided overly strict weeding as a means of crop insurance during years of extreme drought, allowing *S. pumila* to persist and adapt. As a result, the species gradually exhibited traits such as increased plant height, larger spikes and seeds, along with reduced seed shattering—features of progressing domestication.

Through this process, *S. pumila* acquired mimic traits, including elongated leaves, fewer tillers, and taller plant height, particularly when cultivated in *P. sumatrense* fields.

Across 60 strains, *S. pumila* displayed significant morphological and ecological diversity (Figure 35). Notably, domesticated types tended to be taller than the weed types (Figure 35a). Slightly fewer tillers were observed in the domesticated type compared to the weed type, excluding two exceptional strains (Figure 35b). Additionally, the spike length (cm) clearly increased in the domesticated type compared to the weed type (Figure 35c). Meanwhile, the duration to flowering (days) exhibited a bimodal pattern, with early and late forms (Figure 35d). Early domesticated types resembled weed types, while late domesticated types were similar to mimic companion weed types grown alongside other cereals.

The flag leaf length-to-width ratio revealed two distinct trends: some plants had wide leaves, while others had slender leaves (Figure 35e). The last internode diameter (mm) was also noticeably thicker in domesticated types compared to weed types (Figure 35f). Domesticated types mixed with *P. sumatrense* demonstrated higher ratios than other types, which exhibited intermediate ratios. Morphologically, the domestication process was marked by longer spikes had a larger last internode diameter.

Figure 35. ***Setaria pumila*** **panicle types**

a and b, domesticated types (Dk) mixed with *Paspalum scrobiculatum*; c, domesticated type (Ds) mixed with *Panicum sumatrense;* d, weed type shattering seed grains; e and f, cropping fields mixed with *Panicum sumatrense* and *Setaria pumila* at Illur village near Chitoor in Andhra Pradesh.

Table 27. Characteristics of three types in *P. sumatrense* domestication process

Characteristics	Weed type in the field of *P. sumatrense*	Mimic companion weed type to *Pas. scrobiculatum*	Crop type mixed with *Pas. Scrobiculatum*
Seed shattering habit	remarkable	high	low
Spike length (cm)	6.1±0.6	10.4±0.4	11.1±1.3
Spikelet density (grains/cm)	29.0	30.5	33.9
Culm diameter (mm)	under 1	about 1	2
Bristle length (mm)	5.5, dense	6.5, dense	5, sparse
Grain length (mm)	2.0	2.5	3.0
Plant height (cm)	73.8±11.3	90.6±5.1	75.8±5.3
No. of tillers	40.1±10.6	20.0±3.5	43.0±9.7
Flag leaf length	17.1±3.3	22.8±4.5	31.0±4.6
Flag leaf width (cm)	0.5±0.1	0.8±0	1.1±0.1
Days to flowering	51	61	73

S. pumila crop types enhance biocultural diversity by mimicking other grain crops and are sown, harvested, and consumed with *P. sumatrense*. Farmers refer to the mixed grains as *tela samuru* (“white little millet”) in Telugu. In 1997, the proportions of grains purchased at a local market were 70% for *P. sumatrense* and 27% for *S. pumila*. These authors (Kimata et al. 2000) are of the opinion that in severe drought, *S. pumila* provides a reasonable harvest while *P. sumatrense* might fail, supporting the domestication of secondary crops in other cereal fields for arid climates. These grains are used in seven traditional foods, bhat, upma, vada, dosa, *ganji* (thin flour porridge), *kheer* (sweet gruel) and *roti* (unleavened bread; Figure 36) (Kimata and Sakamoto 1992, Kimata et al. 2000).

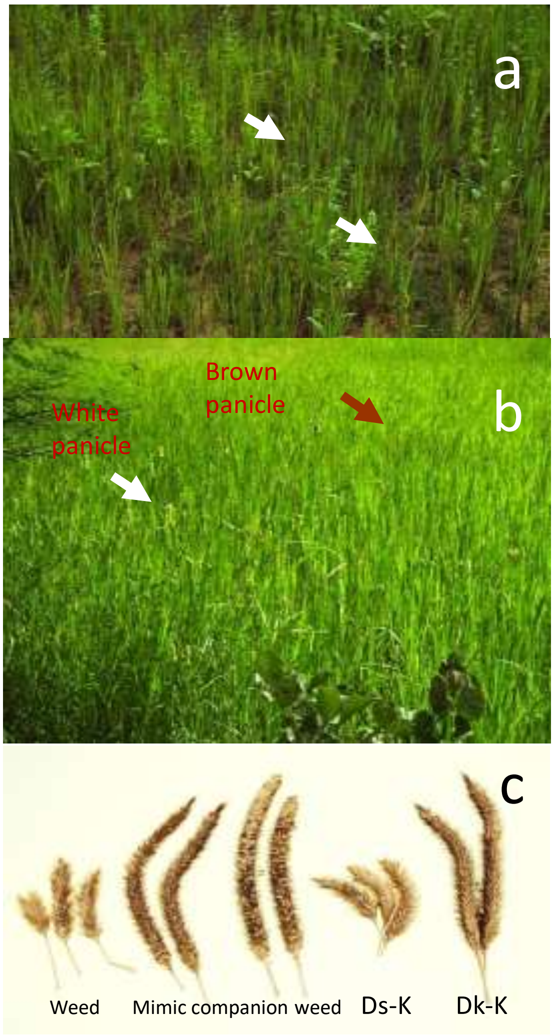


Figure 35. Fields of *Setaria pumila* mixed with *Pas. scrobiculatum* and (a) and *P. sumatrense* (b) in South India; (c) *S. pumila* spikes

Weed; mimic companion weeds; Ds-K, domesticated type mixed with *P. sumatrense*, and Dk-K mixed with *Pas. scrobiculatum* in Karnataka.

Farmers have historically faced significant challenges in differentiating between mimic companion weeds and domesticated types within sympatric fields during the early growing stage. Seed germination in domesticated and annual plants generally occurs rapidly and uniformly, while *Pas. scrobiculatum*, perennial plants, and various weeds exhibit delayed irregular germination.

Meanwhile, *S. pumila* diversified its traits through natural and artificial hybridization in severely arid environments. Mimic companion weeds were harvested together with other millet crops, and inadvertently resown in the subsequent season. Farmers then shifted from hostile weed control measures to more integrative approaches, culminating in recent mixed cropping practices. *S. pumila* is classified as a tertiary crop in relation to associated secondary species, such as *P. sumatrense* and *Pas. scrobiculatum*, particularly when compared with rice cultivation.

Pas. scrobiculatum is characterized by its perennial growth habit and typically exhibits slow seed germination, tillering, and elongation of plant height, allowing distinction from other species. Nonetheless, due to synchronization of certain morphological features—such as plant height and leaf number on the main culm—differentiation among species remains challenging in early growth stage. Domesticated *S. pumila* has adapted morphologically and ecologically to mimic its companion species during early growth, including similarities in leaf and sheath pigmentation. For example, leaf coloration in both *S. pumila* (Ds) and *P. sumatrense* was green (371c–377c), whereas leaf sheath color differed; *S. pumila* was reddish purple (198c–202c), while *P. sumatrense* was green (206c–207c) at site 8 in Andhra Pradesh—a variation that does not suggest mimicry in leaf sheath color based on Panton Formula Guide.

Moreover, *S. pumila* has been domesticated as a tertiary crop following other millet species and upland rice due to its notable drought resistance across the Deccan Plateau. Currently, domesticated *S. pumila* is predominantly cultivated in mixed stands with *P. sumatrense* in South India, while semi-domesticated and mimic companion weed types are grown alongside *P. sumatrense*, *Pas. scrobiculatum*, *E. coracana*, and upland rice in diverse agro-ecological niches in Orissa. The weed type of *S. pumila* is widely distributed throughout the India Subcontinent and across tropical and temperate regions of the Northern Hemisphere. These varieties have successfully adapted to arid conditions and specific agro-ecological niches within the Deccan Plateau, spanning from humid eastern areas to the drier southern regions (Sehgal et al. 1992).

Seed color mimicry between *P. sumatrense* and *S. pumila* was identified in mixed grains at Illur village near Chittoor in Andhra Pradesh (Figure 36a). The pale brown seeds of *P. sumatrense* (Figure 36b) closely resemble those of *S. pumila* (Figure 36c), yet differ markedly from the latter's black seeds (Figure 36d). Despite this similarity, differentiation is possible based on the glossy lemmata in *P. sumatrense*. Indeed, villagers utilize *S. pumila* to prepare three traditional foods: boiled grain (*annamu*), flour porridge (*sankati*), and semi-solid porridge (*uppitu*).

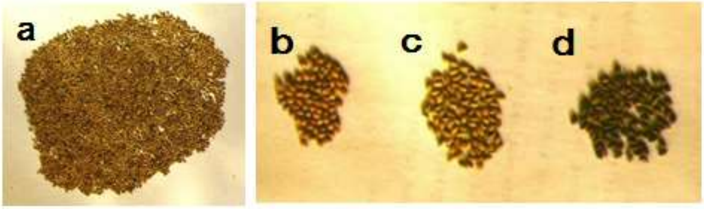


Figure 36. Seed mimicry of *S. pumila* and *P. sumatrense*

a) Mixed grains harvested and sold; b) brown seeds of *P. sumatrense*, c) brown seeds and d) black seeds of *S. pumila*.

Domestication process of *korati, Setaria pumila* based on cluster analysis of morphological traits and AFLP markers

Endemic landraces and related weeds were collected during field surveys in the Deccan region of India since 1983 to elucidate the domestication trajectory of *Setaria pumila* (Poir.) Roem. *et* Schult. (Poaceae) through its mimicry of other grain crops. Comparative investigation leveraging statistical methods and AFLP analyses revealed that domestication of *Setaria pumila* advanced through four distinct stages, shaped by geographical trends in morphological (artificial selection) and genetic variation (neutral DNA markers): weed, companion weed, mimic companion weed, and domesticated type to a secondary crop. The dispersal of paddy rice originated from Assam in the humid east and expanded towards the arid south of the Indian subcontinent, facilitating local farmers' domestication of various millet species as secondary crops along prevailing climatic gradients and dispersal routes. In South India, a domesticated form of *S. pumila* was cultivated only in mixed stands with *Panicum sumatrense.* Around Orissa, other types and related weeds were sympatrically grown with *Paspalum scrobiculatum*, *Eleusine coracana*, and upland rice (*Oryza sativa*) within diverse agro-ecological niches. Accordingly, *S. pumila* has become a tertiary crop among Indian millets, which serve as secondary crops to rice.

Globally, humans have domesticated more than 30 grass species as grain crops, beginning as early as 12,000 years ago. However, several species are now threatened or have ceased to be extensively cultivated, despite their potential nutritional value. This decline stems from the rapid yield improvements of wheat, rice, and maize through technological advances in crop-improvement programs. As cultivation of alternative grains, like millets, diminished during the 20th century, genetic diversity among local varieties has eroded. Recognizing the value of these neglected species as exploitable and underutilized genetic resources is now essential, particularly due to their adaptability to stress-prone environments. In particular, millets—predominantly C_4 plants—are notable for early maturation and resilience under severe drought and intense sunlight.

Small-scale farmers continue to cultivate a few indigenous millet varieties, which represent excellent material for research into crop evolution and the origin and dispersal of domesticated plants. In the Indian subcontinent, certain millet species remain in the process of domestication (Kimata et al. 2000; Singh and Arora 1972). While botanical data largely informs reconstruction of crop evolution, more detailed insights into geographic origins and dispersal can be derived from the basic agricultural complex, comprising cultivation, processing and cooking—collectively reflecting biocultural diversity.

Vavilov (1926) described the domestication sequence from companion weeds associated with wheat to secondary crops within *Avena* and *Secale*. For example, *Secale cereale* L. acquired strong resistance to cold in high-altitude or high-latitude regions, enabling its cultivation under more severe conditions than those under which wheat can grow. Kobayashi (1987, 1989) proposed an integrative model wherein Indian millets (e.g. *P. sumatrense, Echinochloa frumentacea*) transition to secondary crops via mimic companion weeds associated with *Oryza sativa* L. Farmer selection for desirable agronomic traits—such as yield, early maturation, color, sugar content—has guided domestication, although natural selection and hybridization among closely related weeds also occur during this process.

The cultivation range of *O. sativa* extended from wetlands to establish secondarily in uplands within Zomia and the Indian subcontinent, prompting ancestral weedy forms to invade paddy and upland rice fields. Local farmers subsequently domesticated *Panicum sumatrense*, *Paspalum scrobiculatum* and *Echinochloa frumentacea* as secondary crops, given their superior drought resistance relative to upland rice in Eastern India. Several additional millet species were domesticated in this region: *Brachiaria ramosa*, *Digitaria cruciata*, and *Setaria pumila* (Chandra and Koppar 1990; de Wet et al. 1983a, b, c).

Recent archeological studies in the Indian subcontinent have provided useful data on the ancient history of regional grains, with millet materials identified from two archaeological levels in the Southern Neolithic chronology: Phase II (2300–1800 cal BC) and Phase III (1800–1200 cal BC). These materials primarily comprised *B. ramosa* and *Setaria verticillata* (bristly foxtail millet-grass). *S. pumila* appeared in limited quantities, possibly gathered from wild populations (Fuller et al. 2001). Initial occurrences of cereals in the Harrappan Civilization include wheat, barley, and oats in the Early phase (before 2600 BC); *Eleusine* sp. (unconfirmed and problematic, *E. coracana*), *Setaria* sp., and *Panicum* sp. in the Mature phase (2600–2000 BC); and *Paspalum* sp., *Echinochloa* sp., *Sorghum* sp., and *Pennisetum* sp. in the Late phase (post-2000 BC) (Fuller and Madella 2000; Weber 1992).

Advanced molecular techniques utilizing DNA markers, such as SSR (simple sequence repeat), RAPD (random amplified polymorphic DNA), RFLP (restriction fragment length polymorphism), and AFLP (amplified fragment length polymorphism analysis), have been employed for *Setaria* (Benabdelmouna et al. 2001; d'Ennequin et al. 2000; Fukunaga et al. 2002; Lin et al. 2012). Intraspecific polymorphic variability detected through RAPD and RFLP was negligible, whereas AFLP has gained wide acceptance for its high resolution and reproducibility in genetic analyses (Lakshmi et al. 2002), enabling extensive assaying of DNA loci within each reaction using a modest number of primers. Intergeneric polymorphism revealed by AFLP markers was significant (94.4%), while interspecific variation was more moderate; AFLP analysis also showed 66.5% variation between *Panicum miliaceum* and *P. sumatrense* (Bai et al. 1999). Such data on intraspecific diversity and species relationships support continued crop improvement efforts (Lakshmi et al. 2002).

GISH (Genomic in situ hybridization) studies revealed that two diploid species ($2n = 18$), *S. viridis* and *S. italica*, possess genome AA, while the tetraploid species ($2n = 36$), *S. verticillata*, displays an AABB genome structure. Meanwhile, the genomic composition of *S. pumila* (polyploid species, $2n = 18, 36, 72$) remains unidentified (Benabdelmouna et al. 2001).

S. pumila is a cosmopolitan weed distributed worldwide, growing sympatrically on roadsides, uplands, and lowland levees. Four ecological types have been identified based on habitat: the weed type (W), companion weed type accompanied by crops (Wx), mimic companion weed type accompanied by crops (Mx), and domesticated type mixed with crops (Dx). Kimata et al. (2000 and unpublished) documented the biocultural diversity of ecological differentiation within *S. pumila*, including variation in vernacular names (linguistic data). Here, the domestication process of *S. pumila* within the Indian subcontinent is evaluated using cluster analysis of morphological features and AFLP markers.

Materials and Methods

Many local varieties and relative weedy forms of *Setaria pumila* (Poir.) Roem. & Schult. (syn. *S. glauca* [L.] P. Beauv.) have been collected throughout the Indian subcontinent since 1983 via field surveys (Figure 37). Concentrated surveys were conducted in Karnataka, Andhra Pradesh, and Orissa. Concurrently, associated millet and weed species were systematically documented in five plots (1 m^2) at four representative cropping sites using the standard quadrat method. Voucher herbarium specimens and grain samples acquired during these surveys were deposited at Tokyo Gakugei University (Tokyo, Japan) and University of Agricultural Sciences (Bangalore, India). Data regarding agricultural practices, grain processing, food preparation, and local vernacular plant nomenclature was obtained through interviews with local farmers.

The experimental strains (n = 78) were selected from these accessions and cultivated in a controlled greenhouse environment at Tokyo Gakugei University to facilitate comparative analyses of morphological and ecological traits. Additionally, three related species—*S. italica* (n = 6, from Japan), *S. viridis* (n = 2, from Kazakhstan and Uzbekistan), and *S. verticillata* (n = 3, from India)—were grown under identical conditions.

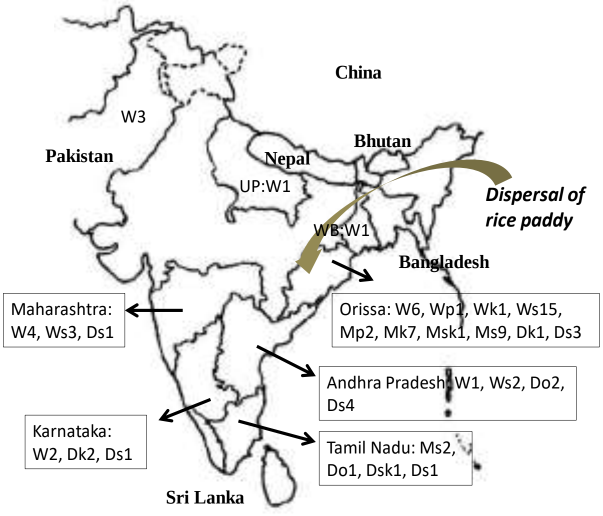


Figure 37. Sites from which *S. pumila* and related species were collected across the Indian subcontinent.

Sixty strains (ten grains each) were sown in a seeding box on June 6, 2012, with 8 cm between rows and 2 cm between seeds. After two weeks, seedlings were transplanted to a greenhouse with 30-cm row spacing and 15-cm plant spacing. Chemical fertilizer (N:P:K = 8:8:5) was supplied at 100 g·m^{-2}. For five *S. pumila* types—three weed (W, Wx, Mx) and two domesticated (Dx mixed with *Paspalum scrobiculatum* and *Panicum sumatrense*)—the following traits were measured at full ripeness: tiller number, plant height, spike length and width, flag leaf length and width, last internode diameter, and duration to flowering. The lowercase character “x” denotes crop mimicry: “p” (paddy, *O. sativa* L.), “k” (*kodora*, *P. scrobiculatum*), “s” (*samai*, *P. sumatrense*), and “o” (others, e.g., *Elusine coracana*). Data analysis used partial correlation coefficients and hierarchical cluster analysis (Ward method) in SPSS version 21 (IBM Corp).

Table 29. *Setaria pumila* materials used

Sample no. & Status	Main crop and remarks	Collection no.	Locality
1Ds-A	*Panicum sumatrense* mixed with *Eleusine coracana*	85-10-31-3-12	Duggamvapalli, Andhra Pradesh
2Ws-M	*P. sumatrense*	k87-9-28-9-4	Kumbharoshi (800m), Maharashtra
3Ws-M	*P. sumatrense*	k87-9-28-9-6	
4Ds-M	*P. sumatrense*	k87-10-1-7-8	16km from Lanja (200m), Maharashtra
5W-M	none	k87-10-3-3-1	Gabi (650m), Maharashutra
6Ws-M	*P. sumatrense*	k87-10-3-5-7	Nadagao village (541m), Maharashtra
7W-M	*Oryza sativa*	k87-10-4-6-7	8km W from Kolhapur (600m), Maharashtra
8W-M	*Setaria italica*	k87-10-5-10-5	Udtare village (652m), Maharashtra
9W-M	*S. italica*	k87-10-5-10-6	Udtare village (653m), Maharashtra
10Ms-O	*P. sumatrense*	k87-10-9-1-1	Sunabeda (895m), Orissa
11Ms-O	*P. sumatrense*	k87-10-9-1-6	
12Ms-O	*P. sumatrense*	k87-10-9-1-7	
13Ms-O	*P. sumatrense*	k87-10-9-1-8	
14Wsk-O	*P. sumatrense* mixed with *Paspalum scrobiculatum*	k87-10-9-2-2	Kundali village (875m), Orissa
15Ws-O	*P. sumatrense*	k87-10-9-5-6	Potang (895m), Orissa
16W-O	none	k87-10-10-2-1	7km from Sunabeda (900m), Orissa
17Ws-O	*P. sumatrense*	k87-10-10-5-5b	2km of Boiparigurha (608m), Orissa
18Ws-O	*P. sumatrense*	k87-10-10-5-6b	
19Ws-O	*P. sumatrense*	k87-10-10-5-10d	
20Ws-O	*P. sumatrense*	k87-10-10-5-13A	
21Ws-O	*P. sumatrense*	k87-10-10-5-13B	
22Ds-O	*P. sumatrense*	k87-10-10-5-14e	
23Ds-O	*P. sumatrense*	K87-10-10-5-16A	
24Ds-O	*P. sumatrense*	k87-10-10-5-16B	
25Ws-O	*P. sumatrense*	k87-10-10-6-8	Beragaon, 12km of Koraput (605m), Orissa
26Mk-O	*Pas. scrobiculatum*	k87-10-11-2-2	Anchalguda village, 20km of Kolaput (870m), Orissa
27Dk-O	*Pas. scrobiculatum*	k87-10-11-2-3	
28Mk-O	*Pas. scrobiculatum*	k87-10-11-2-5	
29Ws-O	*P. sumatrense*	k87-10-11-6-7	Damaniganda village (728m), Orissa
30Ms-O	*P. sumatrense*	k87-10-11-6-8	
31W-O	none	k87-10-12-2-3	Sagada village (240m), Orissa
32W-O	none	k87-10-12-2-7	
33Ws-O	*P. sumatrense*	k87-10-12-5-4	47km NW of Bhawanapatna (690m), Orissa
34Ws-O	*P. sumatrense*	k87-10-12-5-5	
35Ms-O	*P. sumatrense*	k87-10-12-5-7	
36Ws-O	*P. sumatrense*	k87-10-12-5-8	
37Wp-O	*Oryza sativa* mixed with *Pas. scrobiculatum*	k87-10-12-6-2	Balsora village (690m), Orissa
38Mp-O	*O. sativa* mixed with *Pas. scrobiculatum*	k87-10-12-6-3	
39Mp-O	*O. sativa* mixed with *Pas. scrobiculatum*	k87-10-12-6-4	
40Ws-O	*P. sumatrense*	k87-10-12-7-4	Duliguda village,11km of Gopalpur(922m), Orissa
41Ws-O	*P. sumatrense*	k87-10-12-7-5	
42Ws-O	*P. sumatrense*	k87-10-12-8-4	Dakuta (937m), Orissa
43Wk-O	*Pas. scrobiculatum*	k87-10-13-4-14	Puda Pali village (269m), Orissa
44Mk-O	*Pas. scrobiculatum*	k87-10-13-5-6	12km of Kharhiar (272m), Orissa
45Mk-O	*Pas. scrobiculatum*	k87-10-13-5-11	
46W-O	none	k87-10-14-2-1	Mandiapadar village (139m), Orissa
47W-O	none	k87-10-14-2-3	
48W-O	none	k87-10-14-2-4	
49Mk-O	*Pas. scrobiculatum*	k87-10-14-4-3	Budhitadar village (146m), Orissa
50Mk-O	*Pas. scrobiculatum*	k87-10-15-1-6	Ramisarda Tilemal (149m), Orissa
51Ms-O	*P. sumatrense*	k87-10-16-2-3	Kolarapaju village (766m), Orissa
52Ms-O	*P. sumatrense*	k87-10-16-2-4	
53Mk-O	*Pas. scrobiculatum*	k87-10-16-3-4	Bekarakhol village, 30km of Phulabani (522m), Orissa
54Ms-O	*P. sumatrense* mixed with *E. coracana*	k87-10-16-5-4	4km from Tikaball (569m), Orissa
55W-W	none	k87-11-7-0-26	Kalimpong, West Bengal
56Dk-K	*Domesticated type, a few mixed in Pas. scrobiculatum*	96-11-5-1a-2	Kalidevapura, Karnataka
57Ds-K	*A few mixed with P. sumatrense*	96-11-5-2b-6	Madhagiri, Karnataka
58Dk-K	*A little shattering, only one plant mixed with Pas.*	96-11-5-7-2	
59Ds-A	*P. sumatrense*	97-4-12-2-2	Jalaripalli, Andhara Pradesh
60Ds-A	*P. sumatrense*	97-4-12-2-3	
61W-U	weed mixed with *Echinochloa frumentasea*	96-11-17-0-1	Ranichauri, Uttar Pradesh
63Ws-A	*P. sumatrense*	01-10-8-1-5	Mulbagal, Andhra Pradesh
64Ws-A	*P. sumatrense*	01-10-8-2-5	Palmaner, Andhra Pradesh
66Ds-A	*P. sumatrense*	01-10-9-2-4	Dombarpally, Andhra Pradesh
69Ws-O	*P. sumatrense*	01-10-19-2a-3	Polehorebrdle, Orissa
70Ds-T	*P. sumatrense*	85-10-28-1-1	Morumu, Tamil Nadu
71Do-A	mixed stand	85-11-10-1-11	Gandrajupalli, Andhra Pradesh
72Do-A	mixed stand	85-11-10-1-16	
73W-A	mixed stand	85-11-10-1-18	
75W-P	*Vigna mungo*	85-9-15-5-2	39km from Abbottabad to Hazara, Pakistan
76W-P	mixed stand	89-9-29-3-3-5	47km from Muzafabad, Pakistan
762W-P	mixed stand	89-9-29-3-3-6	
77Dsk-T	*P. sumatrense* and *Pas. scrobiculatum*	89-10-25-3-7	Bawalia village, Mandia, Tamil Nadu
81W-K	*S. pumila* ssp. *pallide-fusca*, mixed stand	85-10-16-3-2	Namanahalli, Karnataka
82W-K	*S. pumila* ssp. *pallide-fusca*, mixed stand	85-10-17-3-3	Honnavara, Karnataka
84Do-T	mixed stand	85-10-27-3-6	Vellakadai (Goundar tribe), Tamil Nadu
85Ms-T	*P. sumatrense*	85-10-23-2-15	Kollimalai (Kotha tribe), Tamil Nadu
86Ms-T	*P. sumatrense*	85-10-23-2-7	

Sample number and status: W, weed type; M, mimic weedy medium type; D, domesticated type. Main crop: s, *samai* (*Panicum sumatrense*); k, *kodo* (*Paspalum scrobiculatum*); p, paddy (*Oryza sativa*); o, other species. Locality: A, Andhara Pradesh; K, Karnataka; M, Maharashtra; O, Orissa; P, Pakistan; T, Tamil Nadu; U, Uttar Pradesh; W, West Bengal.

Data analysis

Bands were identified on the gel with Lane Analyzer (ATTO), adjusted as needed, and scored for accessions as present (1) or absence (0). The AFLP marker dendrogram was constructed using neighbor-joining and bootstrap analysis (PAUP* version 4.0) on all data matrices (Nei and Kumar 2000).

Table 29 presents AFLP results for 72 Indian subcontinent accessions, with most bands showing 81.7% to 94.1% polymorphisms; main bands were detected in more than 70% of accessions.

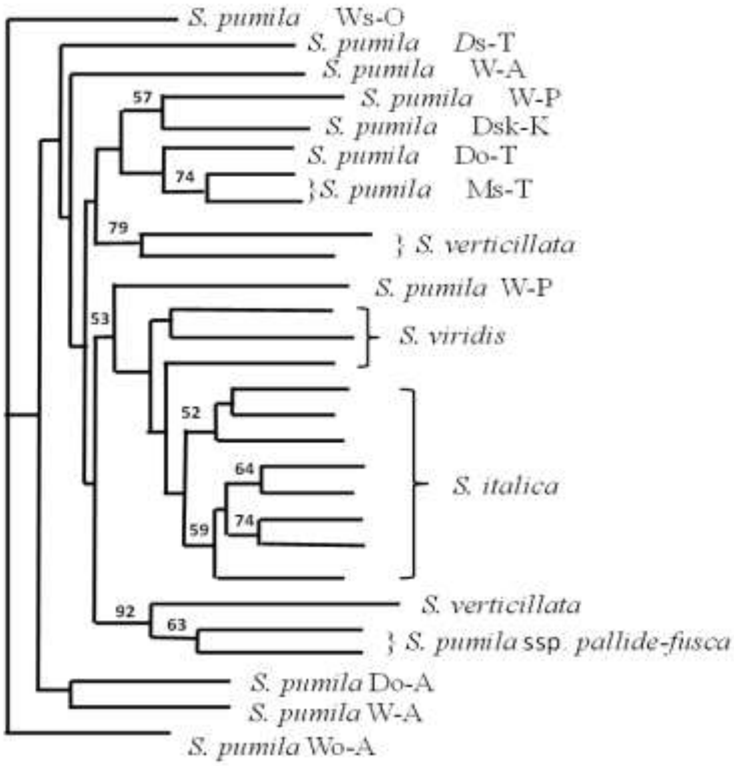


Figure 38. Dendrogram of neighbor-joining method based on AFLP markers of genus *Setaria*.

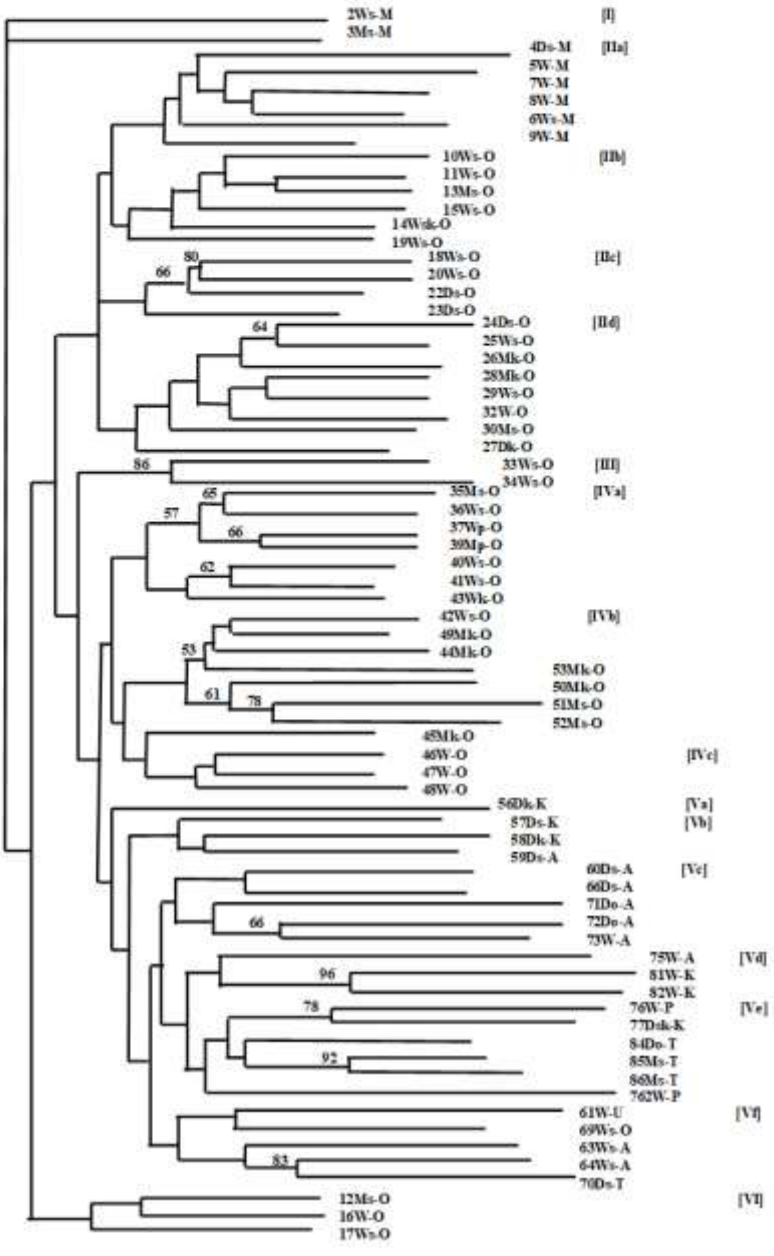


Figure 39. Dendrogram of neighbor-joining method based on AFLP markers of *S. pumila*.

The diversity of AFLP markers was systematically compared among related species (28 accessions) of *S. pumila* (14 including ssp. *pallide-fusca* [2]), domesticated *S. italica* (8 from Japan), the ancestral weed *S. viridis* (3 from Central Asia), and the weed *S. verticillata* (3 from India). The dendrogram generated by neighboring-joint reveals distinct clusters of *S. pumila*, successively, of Ws1 from Orissa; Wo1, Do1, and W1 from Andhra Pradesh; Ds1 from Tamil Nadu; and W1 from Andhra Pradesh (Figure 38). The other clusters included W1 from Pakistan, Dsk1 from Karnataka, and Do1 and Ms2 from Tamil Nadu. *S. pumila* ssp. *pallide-fusca* (2) from Karnataka and *S. verticillata* (1) from Andhra Pradesh formed a cluster. W1 of *S. pumila* from Pakistan, a neighbor of

S. viridis. *S. verticillata* (2), was located in the *S. pumila* cluster, while *S. viridis* (3) and *S. italica* (8) clustered together. Although species positioning within clusters lacked statistical significance at $p \leq 0.05$ (as assessed by the bootstrap test), species categorization remained clear.

Analysis based on AFLP marker data divided *S. pumila* (72 accessions) into six main clusters and 16 sub-clusters (Figure 39). Cluster I contained Ws1 and Ms1 from Maharashtra; Cluster III comprised Ws2; and Cluster VI contained W1, Ws1, and Ms1 from Orissa. These clusters contained no domesticated types. Cluster II (4 sub-clusters, 23 accessions) consisted of: sub-cluster IIa (6) - W4, Ws1, and Ds1 from Maharashtra; sub-cluster IIb (6) - Ws (4), Ms1, and Wsk1 from Orissa; sub-cluster IIc (4) - Ws2 and Ds2 from Orissa; and sub-cluster IId (8) -W1, Ws2, Ms1, Ds1, Mk2, and Dk1 from Orissa. Cluster IV (three sub-clusters, 18 accessions from Orissa) comprised sub-cluster IVa (7) - Wp1, Mp1, Wk1, Ws3, and Ms1; sub-cluster IVb (7) - Ws1, Ms2, and Mk4; sub-cluster IVc (4) - W3, and Mk1. Cluster V (6 sub-clusters, 23 accessions) comprised sub-cluster Va (1) - Dk1 from Karnataka; Vb (3) - Ds1, Dk1 from Karnataka, and Ds1 from Andhra Pradesh; Vc (5) - W1, Do2 and Ds2 from Andhra Pradesh; Vd (3) - W1 from Andhra Pradesh and W2 from Karnataka; Ve (6) - W2 from Pakistan, Ms2, Dsk1, and Do1 from Tamil Nadu; Vf (5) - W1 from Utter Pradesh, Ws1 from Orissa, Ws2 from Andhra Pradesh, and Ds1 from Tamil Nadu.

The domestication processes for these species represent a complex combination of natural and artificial selection, mimicry, hybridization, and polyploidy. Pioneer farmers selected plants demonstrating resilience to environmental challenges (e.g., cold, hot, drought, intense sunlight). Collection of wild cereals remains common in arid regions of Africa and the Indian subcontinent. For instance, *Secale cereale* L. has acquired considerable cold tolerance at higher altitudes or latitudes, allowing its cultivation alongside wheat as a secondary crop in harsh environments (Vavilov 1926). Kobayashi (1987, 1989) proposed an integrated model of the domestication process for several millet species as secondary crops derived from weeds via mimetic association with weeds alongside *Oryza sativa* in the Indian subcontinent.

Key domestication traits include increased seed size and shattering resistance. Partial correlation coefficients examining seed size and shattering demonstrate that artificial selection favored longer cylindrical spikes, thickened final internodes of the main culm, and broader flag leaves to enhance photosynthesis. The low correlation between tiller number and other traits suggests that domestication reduced tiller count in Dk through mimicry of *Pas. scrobiculatum*, whereas tiller number increased in Ds via mimicry of *P. sumatrense*. Selection thus operated in divergent directions (Kimata 2016). Artificial selection also influenced flag leaf morphology, resulting in narrower, earlier-maturing leaves, as supported by the lower correlations between flag leaf measurements and duration to flowering.

A negative correlation between flag leaf ratio (length/width) and plant height demonstrated that, while plant height increased, flag leaves lengthened and narrowed, notably in Ds. *S. pumila* Ds exhibits early maturation and elongated narrow flag leaves, driven by significant negative relationships between these morphological features and flowering time, as well as plant height.

During the evolutionary transition from companion weed to secondary crop—mediated by morphological mimicry of other species (Mo)—*S. pumila* (Ds) developed a slender leaf type characteristic of *P. sumatrense*, whereas *S. pumila* (Do) evolved broader leaves similar to *Pas. scrobiculatum* and other species. According to the Panton Formula Guide (Pantone Inc.) and HPLC anthocyanin profiles (Kimata 2015a), *S. pumila* displays inter- and intra-specific mimetic coloration patterns paralleling those of *P. sumatrense* and *Pas. scrobiculatum*.

Cluster analysis demonstrates that *S. pumila* Cluster I reflects continuous domestication in fields of *P. sumatrense* and other grain crops around the Deccan region. Cluster II, including sub-cluster IIa (Ds1, Ms2, Mk4, Ws3 and W3 from Orissa, Dk2 from Karnataka, and Ws2 from Maharashtra) and sub-cluster IIb (Ms1 and Ws1 from Orissa), offers insights into domestication through mimicry, exemplified by *S. pumila* evolving into Dsk types mixed with *P. sumatrense* and *Pas. scrobiculatum*. Cluster III confirms the broad distribution of *S. pumila* W-type as a cosmopolitan weed across the Indian subcontinent.

The domestication process of *S. pumila* Dsk has proceeded from weed to companion weed, then to mimic companion weed co-occurring with *O. sativa*, *P. sumatrense*, and *Pas. scrobiculatum* in Orissa. The process began with mimic companion weeds (Mks, mainly in Orissa), followed by evolution of the domesticated type (Do), which spread southward to the Deccan Plateau via Andhra Pradesh and subsequently from Dk to Ds in Karnataka and Tamil Nadu.

Continuous natural intraspecific hybridization among weeds, companion weeds, mimic companion weeds, and domesticated forms—evident from regional morphological and genetic biases. Interspecific mimicry was found in the mimic companion weed with *O. sativa*, *Pas. scrobiculatum*, and *P. sumatrense* and other species. Meanwhile, intraspecific mimicry occurred by continuous natural hybridization between weed and domesticated types as well as though natural or artificial selection by farmers. Mimic companion weed types are phenotypically similar to domesticated types but can be distinguished by seed shattering features.

Further comparison of AFLP marker diversity among *S. pumila*, domesticated *S. italica*, ancestral *S. viridis*, and *S. verticillata* (see dendrogram in Figure 38) revealed complex genome constitutions. Recent studies (Wang et al., 2009; Zhao et al., 2013) confirmed diploid (BB) and tetraploid (AABB) forms in *S. verticillata* through GISH, while *S. glauca* (syn. *S. pumila*) carries the "D," genome albeit with unresolved genomic structure. Bayesian dendrograms based on 5S rDNA and *kn1* sequences classified *S. italica*, *S.* viridis, and *S. verticillata* as A-genome taxa; *S. verticillata* as B-genome, and *S. glauca* (syn. *S. pumila*) as D-genome. Geographically, *S. pumila* (W-P) from Pakistan aligned closely with *S. viridis*. *S. pumila* ssp. *pallide-fusca* from Karnataka and *S. verticillata* from Andhra Pradesh. The irregular positions in which *S. pumila* was located were related to polyploid complexity and obscure genomic constitution.

AFLP markers produced highly reproducible bands, with minimal polymorphism within accessions (d'Ennequin et al. 2000). Small millet species including *S. pumila,* display remarkable genetic diversity (Lakshmi et al. 2002) due to its polyploidy and natural hybridization. Although AFLP variation within *S. pumila* is generally high, as indicated by numerous sub-clusters, bootstrap support within sub-clusters is weak. Intraspecific morphological differentiation was readily detected, yet natural hybridization diminishes AFLP variation. Consequently, AFLP dendrograms, which were relatively unaffected by the artificial selection, exhibit clear regional trends: most mimic companion weed accessions aggregate in sub-cluster IVb, while domesticated types predominantly occupy Cluster V, though without strong bootstrap support. Cluster IV, restricted to Orissa, primarily comprises mimic companion weed accessions but lacks domesticated forms. Finally, Cluster II from Maharashtra and Orissa illustrates coexistence of companion/mimic companion weeds and domesticated forms mixed with other crops.

For these polyploid species, the diversity in *S. pumila* has primarily evolved trough mimicry and both inter- and intra-specific hybridization, shaped by natural and artificial selection. The domestication process has contributed not only to adaptation in dry climates but has also fostered a shift in the relationship among weeds, other crops, and farmers, from antagonistic to symbiotic. This evolution highlights the significance of weed–crop complexes and biocultural diversity in plant–human interactions. Therefore, the diversity of *S. pumila* and its relatives should be conserved *in situ* and *ex situ*, particularly in on-farm conservation sites.

Domestication process of *Brachiaria ramosa*

B. ramosa is cultivated primarily under pure single cropping as a sole tertiary crop, while *S. pumila* is cultivated under mixed cropping with *P. sumatrense* as a minor domesticated plant. *B. ramosa* demonstrates greater drought tolerance than *S. pumila*, and has been undergoing specialized adaptation to arid regions, nearly attaining the tertiary domesticated phase. In contrast, the landraces of *S. pumila* have adapted to drier fields in South India than in Orissa. Although *S. pumila* was almost always grown with *P. sumatrense*, it can grow independently if *P. sumatrense* fails during severe droughts, as observed in a 1987 survey, suggesting its potential to become an independent crop (Table 30 and Figure 40).

Table 30. Cultivation and processing of *B. ramosa* and *S. pumila*

Method	Crop	
	Brachiaria ramosa	***Setaria pumila***
Cultivation		
plowing	three time by wooden spade	2~3 times by wooden spade
land grading	twice by wooden harrow	twice by wooden harrow
sowing time	middle August	late September~ealy August
sowing	broadcast	broadcast
croping system	single cropping	mixed cropping with *Panicum smatrense*
manuring	nil or organic fertilizer	organic fertilizer, 700~1000 kg/ha
weeding	nil or once by hands	nil
intertillage	nil or once	nil or once on 10~15 days after sowing
harvest time	end of Octover~early November	end of Octover~midle November
harvesting	ground level harvesting by sickle	ground level harvesting by sickle
Processing		
drying	more than three days~two weeks	eight~ten days
threshing	by stone roller	by cattle tapping
hulling	by stone huller or mechanical huller	by stone mortar and wooden pestle
polishing	by stone mortar	by stone mortar and wooden pestle
milling	by millstone	by millstone and wooden pestle

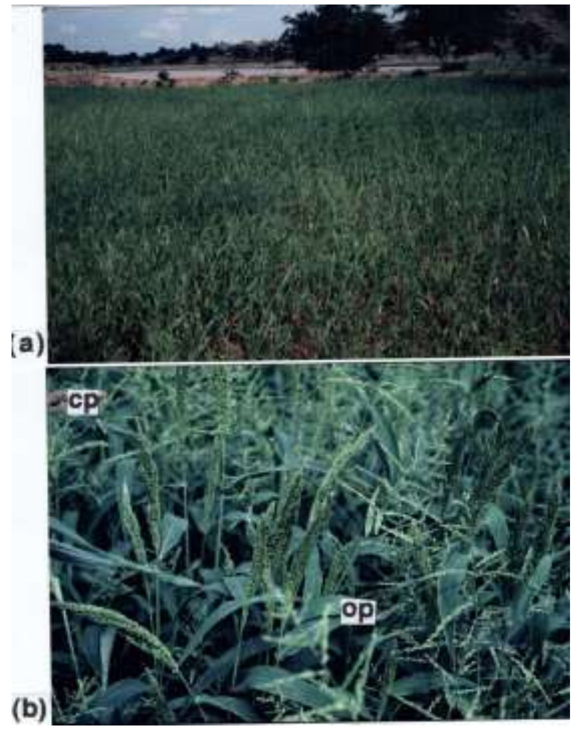


Figure 40. ***Brachiaria ramose***
a, Field at Tumkur, Karnataka; b, compact panicle of crop type (cp)
and open panicle of mimic companion weed type (op).

Domestication process and linguistic diversity of millets

The process of millet domestication is supported by the linguistic distinctions made by farmers through various vernacular names. For example, mimic companion weeds or semi-domesticated plants associated with *Pas. scrobiculatum* are known as *varagu korali*, meaning "the same as kodo millet." Similarly, those occurring with *P. sumatrense* was called *samuru korali*, also indicating a likeness to little millet. The domesticated types are recognized by a range of local names—such as *korati, kora samuru,* and *korin*—which vary according to language and region. This linguistic differentiation underscores the close relationship between naming practices and the domestication process (Chandra and Koppar 1990; Kawase 1987; Kimata et al. 2000, Kimata 2016; Kobayashi 1987, 1989).

Vernacular names for millets have been systematically gathered through field surveys across the Indian subcontinent since 1983. These surveys reveal that farmers possess a nuanced understanding of the status of millets and their related weeds within the domestication process. The dynamic interaction between millets and farmers has been reconstructed by integrating field observations, botanical experiments, archaeological findings, and linguistic data. In regions such as the Eastern Ghats and Southern Deccan Plateau—areas of extensive millet cultivation with related species—a rich diversity of vernacular names has been documented. It is clear that several names originating from old Indo-Aryan and Dravidian languages are closely related to those currently used for millets.

Species such as *Brachiaria ramosa* and *Setaria pumila* have been domesticated from wild weeds that once grew near upland rice fields, primarily through their mimic companion weed forms associated with *Panicum sumatrense* and other grain crops. As a result, *Brachiaria ramosa* has evolved into an independent crop cultivated in pure stands, while *S. pumila* continues to grow as a mixed crop with *Panicum sumatrense* and other millets. Thus, both are considered "tertiary crops," representing a double secondary crop relative to other millets and upland rice. The sequence of millet remnants at historical sites generally corroborates this evolutionary trajectory, with the domestication center encompassing the Eastern Ghats and Southern Deccan Plateau.

Indigenous millets of the Indian subcontinent have been domesticated over approximately 3,500 years (de Wet et al. 1983a; Fuller 2002; Pokharia 2008). These include *Paspalum scrobiculatum* L. (*kodo* millet), *Echinochloa frumentacea* Link (Indian barnyard millet), *Panicum sumatrense* Roth. (little millet), *Brachiaria ramosa* (L.) Stapf. (*korne*), *Setaria pumila* (Poir.) Roem. & Schult. (*korati*; syn. *Setaria glauca* (L.) P. Beauv.), *Digitaria cruciata* (Nees) A. Camus (*raishan*), and *Digitaria sanguinalis* (L.) Scop. (Chandra and Koppar 1990; de Wet et al. 1983a, b, c). The first three species are likely secondary in origin, emerging through mimic and companion weeds of rain-fed paddy and later upland rice in Eastern India. *Brachiaria ramosa* and *Setaria pumila* were subsequently domesticated as secondary crops in South India, associated with other millets via their mimic companion weed types (Kimata et al. 2000; Kimata 2015a, 2015b, Kobayashi 1987, 1989). *Digitaria cruciata* was domesticated in the late nineteenth century by Kashi natives in Meghalaya and is now grown only in the Kashi Hills (Singh and Arara 1972), while *Digitaria sanguinalis* has disappeared, and its origins remain unclear.

Unlike other millets—most of which were likely domesticated in humid eastern regions—*Brachiaria ramosa* and *Setaria pumila* have adapted to the dry climate of the semi-arid tropics. *B. ramosa* was cultivated in the hot, arid red soil zones of southern India, while *S. pumila* was grown in the hot sub-humid ecoregion in red and lateritic soils of Orissa, as well as in the hot semi-arid ecoregion on red loamy soils of Southern India (Sehgal et al. 1992). *B. ramosa* is more drought-tolerant, has specialized adaptation for arid regions, and has nearly attained the tertiary domesticated stage (Kimata et al. 2000). In contrast, local varieties of *S. pumila* have adapted to drier fields in Southern India compared to Orissa. Although typically grown with *Panicum sumatrense*, *S. pumila* can be cultivated independently in severe drought conditions, as observed during the 1987 survey, suggesting its potential to become a sole crop.

Currently, *B. ramosa* is an underutilized millet, with cultivation largely restricted to the dry districts Tumkur and Anantapur bordering Karnataka and Andhra Pradesh. It is grown as a sole tertiary crop in pure stands, whereas *S. pumila* remains a minor domesticated plant, typically grown in mixed cropping systems with *P. sumatrense* and other grains.

The "basic agricultural complex," or the "from seeds to stomach" concept, introduced by Nakao (1967), emphasizes that domesticated plants are inherently linked to a broader cultural complex—including cultivation techniques, processing, culinary use, religious practices, and vernacular names (Kimata and Sakamoto 1992). Bellwood and Renfrew (2002) proposed and examined the "farming/language dispersal hypothesis" across archaeology, linguistics, and genetics from a broad comparative perspective. Each millet and its related weed possesses multiple vernacular names across different localities and languages.

This study focuses on reconstructing the domestication process, particularly for *B. ramosa* and

S. pumila, through an analysis of vernacular names, informed by linguistic archaeology, in light of the scarcity of comprehensive linguistic data for indigenous millets (Fuller 2002; Southworth 2005).

B. ramosa was primarily cultivated in select states of South India characterized by the savanna climate of the Deccan Plateau. Both *B. ramosa* and its relatives are summer annuals and are known by numerous vernacular names across different regions and languages (Table 31). This domesticated type, for example, is referred to as *hama pothaval* in Maharashtra, *chama pothaval* in Kerala, and *kama pampul* and *palapul* in Tamil Nadu. In the border areas between Andhra Pradesh and Karnataka, names such as *korne*, *korneki*, *andakora*, as well as *pedda sama* and *disakalu,* are used. The mimic companion weed type is known as *koothi same*, *sakalati same*, and *pil same* in Tamil Nadu, while the weed type is known as *gusara pata* and *chusara mata* in Orissa, and *akki hullu* and *votlu kosavu* in Andhra Pradesh (cf. Chandra and Koppar 1990; Kawase 1987; Kimata et al. 2000; Kobayashi 1987, 1989).

Table 31. Vernacular names for *Brachiaria ramosa*

State	Language	Status	Vernacular names
Orissa	Oriya	Weed with *Pas. scrobiculatum*	gusara pata, chusara mata
		Weed/Domesticated?	ghusara pata, lota, ghada langi
Maharashtra	Marathi	Domesticated	chama pothaval 3)
Andhra Pradesh	Telugu	Weed	akki hullu, votlu kosavu
		Domesticated	andakora, anda korra, *pedda sama* 1), disakalu, edurigaddi
Karnataka	Kannada	Domesticated	kornne, korale, korne, korneki, kornike, bennakki hullu 3)
Tamil Nadu	Tamil	Mimic companion weed with *P. sumatrense*	koothi same, sakkalati same, *same melatti* 5), pil sama, pani varagu
		Domesticated	kam pampul, palapul 3)
Kerala	Malayalam	Domesticated	chama pothaval 3)

Italics cited from 1) Fuller 2002, 2) Kobayashi 1991, 3) Ambasta 1986.

Setaria pumila is cultivated at multiple hill sites, particularly across Orissa and southern India. Thes semi-arid regions, including the Deccan Plateau, are characterized by a savanna climate. *S. pumila* and its related species are summer annuals known by a diverse array of vernacular names that vary according to region and language (Table 32). The domesticated type of *S. pumila* is called *nehari* in Orissa, *lingudi* in Maharashtra, *korati* in Andhra Pradesh, *korlu* in Tamil Nadu, and *korin* in Karnataka (cf. Chandra and Koppar 1990; Kawase 1987; Kimata et al. 2000; Kobayashi 1987, 1989). In certain instances, the names comprise two words, such as *kuku lange* and *kukur lange* in Orissa, *kora samuru* in Andhra Pradesh, and *samuru korra* in Karnataka.

The mimic companion weed type of *S. pumila* also possesses a wide range of local names, most commonly consisting of a single word. Examples include *nauri* in Bihar and Madhya Pradesh, *lingri* in Orissa, *korale* in Andhra Pradesh, and *erikorra* in Karnataka. Some names feature adjectives that reference associated plants; for example, in Andhra Pradesh, *varagu korali* and *varagu sakkalathi* are used for weeds growing alongside *kodo* millet, while *samalu korali* and *arasama* denote companion weeds of little millet. The weed type is commonly called *navari* in Madhya Pradesh, *ghas* in Orissa, and has unique names such as *ghoda langi* ("horse tail") in Orissa and *sana korulu* ("little foxtail millet").

Table 32. Vernacular names for *Setaria pumila*

State	Language	Status	Vernacular names
Bihar	Hindi	Mimic companion weed with *Pas. scrobiculatum*	nauri, navri, nebri, neuri, nevri, nibri, harri, tutuam
Orissa	Oriya	Weed	ghoda langi, kukulange, birailange and gaso(Kondha), ghas; *bilai lange* and *lota* 2)
		Mimic companion weed with *E. coracana, Pas. scrobiculatum, P. sumatrense* and *Oryza sativa*	lingri, ghas lingudi, kukuru lange; *ghas lingri* 2)
		Domesticated type with *Pas. scrobiculatum* and *P. sumatrense*	nehari, kuku lange, kukur lange (Konda Dora), kukuru range; *kukuru lange* 5), kuku lange, lingudi, lengudi, kukukangdi
Madhya Pradesh		Weed	navari, navri, naviri (Variga)
		Mimic companion weed with Pas. scrobiculatum	*harri, nauri, navri, neuri, nibri, tutuam, nebri* and *nevri* 2)
Maharashtra	Marathi	Weed	ghas lingudi
		Domesticated type	lingudi, lengudi
Andhra Pradesh	Telugu	Weed	sana korulu
		Mimic companion weed with *Pas. scrobiculatum* and *P. sumatrense*	korale, kurale, kurule kaddi, korinlu, samuru korali, arasama, varagu korali, varagu sakkalathi
		Domesticated type	korati, korindlu, korinlu, koral, kora samuru, same korulu, samelu, sama, arasama, chinna sama, tela samuru, nerige, nerigalu, *samuru korra* 2)
Tamil Nadu	Tamil	Domesticated type	korlu, korati
Karnataka	Kannada	Mimic companion weed with *E. coracana, Pas. scrobiculatum, P. sumatrense* and *Oryza sativa*	erikorra, korindulu, arasama, nerigalu, neriya
		Domesticated type with *P. sumatrense*	korin, korra, korrulu, samuru korra
Others	Hindi	Domesticated type	*bandhra* 1)

Italics cited from 1) Fuller 2002, 2) Kobayashi 1991.

Austin 2006: *korai* [*kora, korali*] (Bengali, Deccan, Hindi, India and Bangladesh), *bandra* (Hindi, India), *varagu korali* (*varagu*, firewood, *korali*, ear or corn, Tamil)

The vernacular names of other indigenous millets and rice in the Indian subcontinent are presented in Table 33. The domesticated type of *Panicum sumatrense*, a summer annual, is typically called *samai*, *same*, *sama*, and similar names in South India; *vari* and *wari* in Maharashtra; *gurji* and *koeri* in Orissa; and *gondula* in West Bengal. Indigenous communities refer to it as *kutki* (Vaiga) and *mejheri* (Gobdi) in Madhya Pradesh; *gundli* (Munda) in Bihar; *ghantia* (Kunda Tading), *gurgi* (Kunda Dora), and *suau* (Paraja) in Orissa; and *batta* (Kotha) in Tamil Nadu. The mimic companion weed type is called *akki marri hullu* ("weed-like rice"), *kadu same* ("weed little millet"), and *kosu samalu* only in Karnataka; elsewhere, it is sometimes called *kadu* and *fodo* in Karnataka, *gabat* in Maharashtra, and *erigola* and *arasama* in Andhra Pradesh.

Table 33. Vernacular names for other indigenous millets and rice

Country State Growth habit	Language	Status	Vernacular names (Indigenous people)					
			Panicum sumatrense	*Paspalum scrobiculatum*	*Echinochloa frumentacea*	*Digitaria curuciata*	*Coix lacryma-jobi*	*Oryza sativa*
			summer annual	perennial	summer annual	summer annual	perennial	perennial
Pakistan								
NWFP								chawl
Gilgit								
Baltistan								
Punjab					*sarou* [4], *swank* and *sawank* [6]			
Baluchistan					*sawara* [6]			
India								
Jammu & Kashimir		domest			*karin* [4]			
Himachal Pradesh		domest		katai				
Uttar Pradesh	Hindi	domest		koda				dhan
(Uttaranchal)		domest			jhangora, jangora, madira			dhan
Punjab		domest	*kutki* [4]	*kodora* [4]				
Haryana								
Rajasthan								
Gujarat		domest		*menya* [4]				
Madhya Pradesh		weed			chichvi = *E. colona*		gulru = *C. gigantia*	pasahi =*O. rufipogon*
		comp. weed		kodo, *kodaira, kodaila and marendo* [2]	chichvi, *nauri* [2]			
		domest	kutki (Vaiga), mejheri (Gondi, Kal and Vaiga)	kodo	sawan, savan, sawai			dhan, chawal, lehi = upland rice
Maharashtra	Marathi	wild		kotcha				deobath =*O. rufipogon*
		weed	gabat		sankari wari			
		domest	vari, wari, nagri, sama, varag, kodra, warai [2]	kodo, kodora, harik	wari			tandul
Bihar (Jharkhand)	Hindi	wild		khar sami = *Pas. indicum, kodo wani; matwani* and *kharasami (Pas. sp.)* [2]	sain		gurya	
		comp. weed		kodo war, *marendo* [2]				
		domest	gundli (Munda)	kodo (Munda)	sawan, swan, sama			chawal, dhan, gora-dhan = upland rice
Orissa (Chattisgarh)	Oriya	weed		kodo-ghas, goddo	dhela = *E. colona*		korankhar = *C. gigantia,* gorigodio	balunga
		comp. weed		*kodoghas* (Paraja), *mandia* and *kodo* [2]				
		domest	gurji, koeri, suan	kodo, koddo, koda	jhari, dhatela			dhan, gadeba dhan = upland rice
	Others	domest	ghantia (Kunda Tading),gurgi (Kunda Dora), suau (Paraja), nalisuan, kusuda, kosula (Others)		gruji suau (Paraja)			
Andhra Pradesh	Telugu	weed	ara sama, erigola					
		domest	same, sama, samuru, *nella shama* [4]	arika, *allu* [4]	ooda, oodalli, *bouth-shama* [4]			paddy, biyyam
Tamil Nadu	Tamil	domest	sawa, sama, samuru, samai, *cha'mai* and *shama* [6], batta (Kotha)	varagu, *waragu* [2], *kodra* and *harik* [2]	kudurai-vali, korali		kassaibija [4]	paddy
Karnataka	Kannada	weed	kadu, fodo					
		comp. weed	akki marri hullu, *akki hullu, kavadadara hullu, kaddu same, kosu samalu* and *yerri arasamulu* [2]					
		domest	same, sawan, sami, hejjanve, *pani varagu* and *samulu* [2]	varagu, arka, alka, kodo	wadalu			gouri
Kerala								
West Bengal	Bengali	weed/ domest			*shama = E. colona* [4]		garemara = *C. gigantia*	
		domest	*gondula* [4]	*koda* [4]	*sama* and *kheri* [4]		*gurgru* and *kunch* [4]	
Megaraya	Khasi	domest				raishan		
Nagaland		domest					*re-si'* [4]	chahau
Others	Hindi	domest	*shavan* [1], *kutki* and *gundli* [4]	*kodu* and *kodhra* [1], *kodaka* [4]	*sa'nwa, sa'muka* and *sawa* [4], *shama, sanwa* and *sawank* [1]		*gurlu, giral* and *garahedua* [1], *kauch-gurgur, saukru'* and *lechusa* [4]	*vrihi* [1]
	Sanskrit	domest		*kora'susha* and *kodrava* [4]				
	NW Province	domest		*kodon* and *marsi* [4]	*sarwak* and *shamak = E. colonum* [4]			
	Deccan	domest			*kathli* [4]			
	unknown	domest						
Nepal	Nepalese	weed			sama and ketu (Newar) = *E. oryzicola*			
		domest		kodra				dhan, paddy
Bhutan	Bhutanese							
Bangradesh		domest						
Sri Lanka	Sinhalese	domest	*mene'ri* [4]	*wal-amu* [4]	*wel-marukku* [4]		*ki'kir-rindi'* [4]	

Italics cited from 1) Fuller 2002, 2) Kobayashi 1991, 4)Church 1886, 6) Kawase 1991, ..

The domesticated type of the perennial *Paspalum scrobiculatum* is primarily called *kodo*, *kodora*, and similar names, with regional variants such *harik* in Maharashtra; *arik* in Andhra Pradesh; *arka*, *alka*, and *varagu* in Karnataka; and *varagu* in Tamil Nadu. The mimic companion weed grew in upland rice fields is called *kodo* and *kodaira* in Madhya Pradesh, *kodo war* in Bihar, and *kodoghas* (Paraja) in Orissa. The wild/weed type is called *kotocha* in Maharashtra, *khar sami* and *kodo wani* in Bihar, and *kodo ghas* in Orissa.

The domesticated summer annual *Echinochloa frumentacea* is called *jangora* in Uttar Pradesh; *sawan* and related names in Madhya Pradesh and Bihar; *sankari wari* in Maharashtra; *jhari*, *dhatela*, and *gruji suau* (Paraja) in Orissa; *ooda* in Andhra Pradesh; *kudurai vali* in Tamil Nadu; and *wadalu* in Karnataka. Its ancestral weed, *Echinochloa colona,* is referred to as *chichivi* in Maharashtra, *dhela* in Orissa, and possibly *sain* in Bihar.

The summer annual *Digitaria cruciata* species is exclusively called *raishan* in Kashi Hills. Meanwhile, the domesticated perennial *Coix lacryma-jobi* is called *re-si* in Nagaland (Church 1886), whereas its weedy relatives, which often invade rice paddy fields, are called *gulru* in Madhya Pradesh, *gurya* ("small") in Bihar, *korankhar* in Orissa, and *garemara* in West Bengal.

The perennial rice variety *Oryza sativa* L. is commonly called *chawal* or *dhan*, with upland rice receiving specific names, such as *lehi* in Madhya Pradesh, *gora dhan* in Bihar, *gadeba dhan* in Orissa, and potentially *gouri* in Karnataka. Its wild relative, *O. rufipogon* Griff., is especially used for festival food and is known as *pasahi* in Madhya Pradesh, *deobath* in Maharashtra, and possibly *balunga* in Orissa.

Table 34 presents the vernacular names of summer annual Asian and African millets in the Indian subcontinent. *Panicum miliaceum* L. is commonly called *cheena* and similar names, with some regional variations, such as *wari* and *tane* in Maharashtra and *varagu* in Orissa, Andhra Pradesh, Tamil Nadu, and Karnataka.

Setaria italica (L.) P. Beauv. is also widely called *kangani*, *kauni*, and similar Sanskrit names, while it is called *rala* and *rai* in Maharashtra, *korra* and *navane* in Andhra Pradesh, *korra* and *thenai* in Tamil Nadu, and *navane* in Karnataka.

Eleusine coracana Gaertn. is generally called *ragi* in Madhya Pradesh, Orissa, and South India, *mandua*, *marwa*, and similar names in Uttar Pradesh and Bihar, *natuni* and similar names in Maharashtra and Karnataka, *tamada* in Andhra Pradesh, *kapai* in Tamil Nadu, and *kodo* and similar names in Uttar Pradesh, West Bengal, and Nepal. Indigenous communities call it by various names, including *manje suau* (Paraja), *mandia* (Kondho), and *pahado mandia* (Kond Dora) in Orissa.

Sorghum bicolor Moench is generally called *jowar*, with regional names like *cholam* in Tamil Nadu, *junero* in West Bengal, and *junero makai* in Nepal.

Pennisetum glaucum (L.) R. Br. is commonly called *bajra* and similar names, but it is sometimes called *kayna* in Orissa, *sajja* in Andhra Pradesh, and *cumba* and similar names in Tamil Nadu.

Table 34. Vernacular names for Asian and African millets in the Indian subcontinent

Country State Growth habit	Language	Status	Vernacular names (Indigenous people)				
			Panicum miliaceum summer annual	*Setaria italica* summer annual	*Eleusine coracana* summer annual	*Sorghum bicolor* summer aannual	*Pennisetum glaucum* summer annual
Pakistan							
NWFP			*olean* [6]	*ghgh, ghok, gokhton, gokhtan, grashik, grach, gras* and *grass* [6]			bajera, baijera
Gilgit			*olean, chiena, cheena, bau* and *onu* [6]	*gras, cha, cheng* and *cheena* [6]			
Baltistan			*tzetze* [6]	*cha* [6]			
Punjab				*kangani, kangni* and *kongoni* [6]	*mandoh* [6]	jowar, *jowari* [6]	bajra,
Baluchistan							
India							
Jammu & Kashimir	Kashimiri						
Himachal Pradesh			charai	kauni			
Uttar Pradesh	Hindi	weed			*khadua* = hybrid by *E. indica* [2]		
		comp. weed			*jhhadua* = hybrid by Indaf [2]		
		domest	china, sawan	kangani, kangooni	mandua, ragi	jowar, jwar, juara	bajra
(Uttaranchal)		domest	cheena, chin	kauni, kouni, korin, konin	mandua, manduwa, marwa, koda		
Panjab	Panjabi						
Haryana							
Rajasthan							
Gujarat	Gujarati						
Madhya Pradesh		wild/weed					
		domest		kang, kakun	ragi, madia	jowar	bajira
Maharashtra	Marathi	wild/weed			nachuni = *E. indica*		
		domest	wari, tane	rala, rai	nachani, nachuni, nachana, ragi	jowar, jowari, jowary	bajeri, bajri
Bihar (Jharkhand)	Hindi, Bihari	weed			*marwani, malwa* =*E. indica* [2]		
		domest	cheena	kauni	marua, maruwa, *malwa*	jowar	bajera
Orissa (Chattisgarh)	Orya	wild/weed			jangali-suau (Paraja) = *E. indica*		
		domest	pani-varagu, cheena	kangu, gangu	ragi, manje-suau (Paraja), mandia (Kondho), pahado-mandia (Kond Dora)	jonna, jhna, jowary, jowar	kayna
	Others	domest		kangul (Paraja)			
Andhra Pradesh	Telgu	domest	variga	korra, kora, koralu, navane	ragi, tamada	jonna, jower	bajera, sajja, *gantilu’* [4]
Tamil Nadu	Tamil	domest	pani varagu, *varagu* and *katacuny* [4]	thenai, korra, *thennai* [1], *tinai* [4]	ragi, kapai	jowar, jara, jora, cholam	bajera, cumba, cumbu, *cumbu’* [4], *kambu* [6]
Karnataka	Kannada	weed			*kadu ragi, ragi kaddi,* = *E. indica* [2]; *hullu* = hybrid by Indaf [2]		
		domest	baragu	navane, nawane	ragi, nachina	jowar	bajra
Kerala							
West Bengal	Bengali	domest	*cheena* [5]	*ka’kun* [4]	kodo	jowar, junero	
Others	Hindi	domest	*chin, morha* and *anu* [1], *chena* and *chi’na* [4], *cheena* [5]	*kangni, kangu* and *kakun* [1], *ka’ngni, ta’ngan, kayuni* and *rawla* [4]	*ragi* [4]		*ba’jra, ba’jri* and *lahra* [4]
	Sanskrit	domest	*vrihibheda* [4], *u^nu^* and *vreelib-heda* [5]	*ka’ngu* and *priyangu* [4], *kungu^* and *priyungu^* [5]			
	unknown	domest	*sa’wan-jethwa, kuri, phikar, ra’li* and *bausi* [4], *worga* (Telinga) [5]			*joa’r* [4]	
Nepal	Nepalese	domest	china	kauni, kaoni-tangure	kodo	junero-makai	bajra
Bhutan	Bhutanese						
Bangradesh				kaaun			
Sri Lanka	Sinhalese			*tana-ha’l* [4]			

Italics cited from 1) Fuller 2002, 2) Kobayashi 1991, 4) Church 1886, 5) de Candole 1989, 6) Kawase 1991.

Table 35 presents a summary of the vernacular names for other major cereal crops. *Triticum aestivum* L., commonly known as wheat, is referred to *gehun*, *godi*, and other similar names. *Triticum dicoccum* Schübler, Char. et Descr., another wheat species, is known as *gangil* in Tamil Nadu and *aja* in Karnataka. *Hordeum vulgare* L., a winter annual plant, is called *jao* and similar names. *Avena sativa* L. is not cultivated in South India. *Zea mays* L., a summer annual, is widely called *makai* and similar names, while its wild ancestor teosinte, which was introduced as a fodder crop, is called *jenera* in Bihar.

Table 35. Vernacular names for other cereals in Indian subcontinent

Country	**Language**	**Status**	**Vernacular names** (Indigenous people)			
State			***Triticum aestivum***	***Hordeum vulgare***	***Avena sp.***	***Zea mays***
Growth habit			**winter annual**	**winter annual**	**winter annual**	**summer annual**
Pakistan			ghandam, suji			makai
India						
Jammu & Kashimir						
Himachal Pradesh						makka
Uttar Pradesh	Hindi	domestic				makai, makka, maki
(Uttaranchal)		domestic	gehun			makka
Punjab						
Haryana						
Rajasthan						
Gujarat						
Madhya Pradesh		wild/weed				
		domestic	gahun	jao		makai
Maharashtra	Marathi	wild/weed				
		domestic				makka
Bihar (Jharkhand)	Hindi	domestic				makai, jenera = teosint
Orissa (Chattisgarh)	Orya	wild/weed				
		domestic	ghaun, gahomo			makka
Andhra Pradesh	Telgu	domestic				
Tamil Nadu	Tamil	domestic	godi, gangil = *T. diccocum; godome, kothimai and kothi* [4]	gangi		
Karnataka	Kannada	domestic	aja = *T. diccocum*			makai
Kerala						
West Bengal	Bengali	domestic				
Megaraya						
Nagaland						
Others	Hindi	domestic				
	unknown	domestic				
Nepal	Nepalese	domestic	gaun, tro	jau, ne, uwa (Sherpa)		makai
Bhutan	Bhutanese					
Bangradesh						
Sri Lanka	Sinhalese					

The wild ancestors of Indian millets primarily occupied wet habitats, including the margins of ponds and riverbanks, and frequently established themselves within rice paddy fields. In regions, such as Pakistan, Nepal and India, numerous Poaceae grass species are prevalent within paddy fields and levees. Over time, these weeds coexisted within rice paddies and upland fields, forming sympatric communities and ultimately evolving into companion weeds, which underwent further adaptation by mimicking the morphological and ecological traits of rice, leading to their recognition as mimic companion weeds.

The relationship between these plants and farmers gradually evolved from an initial, subconscious antagonism toward a more collaborative relationship. Farmers began to use them as sources of fodder and as insurance crops within semi-domesticated systems, reflecting a symbiotic association. Gradually, certain species transitioned to being independently cultivated for food grains, marking their full domestication. This evolutionary process fostered a symbiotic relationship between the plants and farmers (Kimata 2015a, 2015b).

Two types of mimicry are observed in this process: inter-specific mimicry, where different species serve as companion weeds, and intra-specific mimicry, which arises through hybridization between domesticated forms and closely related weed types.

Linguistic differentiation among local communities provides further evidence for the domestication process. A wide range of categories—such as weed, companion weed, mimic companion weed, semi-domesticated, and domesticated types—are recognized in vernacular names for species such as *Brachiaria ramosa* and *Setaria pumila* (Tables 31 and 32). For instance, in Jalaripalli Village, Andhra Pradesh, *Setaria pumila* mixed with little millet is called *kora samuru* ("foxtail millet-like little millet") and *tela samuru* ("grains mixed with little millet"). This nomenclature illustrates that *Setaria pumila* functions agro-ecologically as a secondary origin (Kimata et al. 2000).

The vernacular names of *Panicum sumatrense* and *Paspalum scrobiculatum* also help distinguish different stages in their domestication process. For example, mimic companion weed types are known as *akki hullu* (little millet), meaning a rice-like weed, and *kodoghas*, meaning a kodo millet-like weed in upland rice fields (Kobayashi 1991). These linguistic distinctions support the view that both species evolved as secondary crops through a mimic companion weed stage in upland rice fields.

Similarly, local naming practices for *Echinochloa frumentacea* and its ancestor *Echinochloa colona* are precise (Yabuno 1962). In Orissa, they are called *jhari* and *dhela*, respectively (Table 35). Names such as *same* and *sawan* are occasionally used for both *Panicum sumatrense* and *Echinochloa frumentacea*, although not simultaneously or in the same locality.

Analogously, regional terms for *Eleusine coracana* distinguish it from *Eleusine indica* and their hybrids. However, some weeds associated with millets and cereals do not possess specific vernacular names (Tables 36). Notably, *Panicum miliaceum* and *Setaria italica* are identified by a variety of names across regions such as the North–West Frontier Province and Gilgit in Pakistan (Kawase 1991). In south India, the vernacular names for culinary millets are particularly distinctive, reflecting the regional predominance of rice and wheat as staple foods elsewhere (Kimata 1991).

Archaeological linguistics provides further insight into the domestication of millets (Table 36). Notably, old Indo-Aryan names for *Brachiaria ramosa*, *Setaria verticillata*, *Setaria pumila*, and *Panicum sumatrense* are not found in ancient literature (cf. Southworth 2005), suggesting their relatively recent domestication in India. Conversely, terms such as *kodorava* for *Paspalum scrobiculatum* are considered to be the origin of *kodo* and *kodora*. Additionally, *syamaka* for *Echinochloa frumentacea* is derived from *shama* and *sama*; *cina(ka)* for *Panicum miliaceum* is related to the origin of *cheena*; and *kanku(ni)* and *rahala* for *Setaria italica* correspond to the common term _kangani_ and _rala_ in Maharashtra. The term _madaka_ for _Eleusine coracana_ is the origin of _mandua_ in Uttar Pradesh, while *_bajjara_ is the origin of _bajra_ (*, reconstructed forms by Southworth 2005).

Dravidian linguistic roots, such as *_var-ak-_ for _Paspalum scrobiculatum_ and _Panicum miliaceum_ is considered to be the origin of _varagu_, while *_tinai_ and *_nuv-an-ay_ for _Setaria italica_ evolved into _thenai_ in Tamil Nadu and _navane_ in Andhra Pradesh and Karnataka.

These etymological connections, rooted in old Indo-Aryan or Dravidian languages, suggest either an earlier introduction from western regions or long-standing domestication within India, a conclusion supported by archaeological evidence (Weber 1992).

Table 35. Summary on linguistic archaeological names for millets and other cereals

Species name	English name	Old Indo-Aryan	Dravidian	Others
Brachiaria ramosa	browntop millet	?	see Table 1	
Setaria verticillata	bristly foxtail	?	?	
Setaria pumila	yellow foxtail	?	see Table 2	
Panicum sumatrense	little millet	?	see Table 3	
Paspalum scrobiculatum	kodo millet	_kodrava_	_*ar-V-k-, *var-ak-_	_*var-ak-_ (Tamil, Malayalam, Kannada), _*ar-Vk-_(Kannada, Telugu)
Echinochloa frumentacea	Sawa millet	_syamaka_	see Table 3	
Digitaria cruciata	Khasi millet	nil	nil	see Table 3
Coix lacryma-jobi	Job's tear	nil	?	
Oryza sativa	rice	_vrihi_	_*var-inc_	see Table 3
Oryza rufipogon	wild rice	_nivara_	_navarai/nivari_	see Table 3
Panicum miliaceum	common millet	_cina(ka)_	_*var-ak-_	_*ə-rig_ (Proto-Munda), _*var-ak-_ (Telugu)
Setaria italica	foxtail millet	_kanku(ni), *kangu(ni), tanguni, (rahala)_	_*kot-, *tinai, *tin-ay, *nuv-an-ay_	_*kam-pu_ (Tamil, Malayalam), _*ar-Vk-_ (Kannada, Gondi/Gorum, Kuwi),
Eleusine coracana	finger millet	_madaka_	_*arak/*arak-_	_deray_ (Kherwarian Munda),
Sorghum bicolor	sorghum	_yavanala, yavakara_	_*conn-al_	_*gang(-)gay_ (Proto-Munda)
Pennisetum glaucum	pearl millet	_*bajjara_	_*kampu_	_*kam-pu_ (Kannada, Telugu)
Triticum aestivum	wheat	_godhuma_	_*kul-i_	_godi_ (Kannada),
Hordeum vulgare	barley	_yava_	_*koc-/*kac-_	_kaj_ (Kota/Konkani), _koj_ (Toda), _gajja_ (Prakrit)
Avena sativa	oat	?	?	see Table 5
Zea mays	maize	nil	nil	see Table 5

Modified and based on F.C. Southworth (2005)

Reconstructed forms are conventionally preceded by astarisks to denote non-attestation (Southworth 2005)

Table 36 summarizes the naming scheme for millets and their relative weeds, illustrating how farmers recognize four stages in their relationships with these plants.

Table 36. Naming scheme for millets and weeds by farmers

Stage	Awareness	Typical cases (species name) [meaning]
I	Unknown	no name: ghas, hullu [weed]
II	Non distinctive	the same name of crop as weed: ragi, malwa (*Eleusine coracana*)/ragi, malwa (a weed, *E. indica*) kodo (*Paspalum scrobiculatum*) /kodo (the weed) kukuru lange (*Setaria pumila*)/kukury lange (the mimic weed)[dog's tail]
III	Identified	
1.	**a specific word** (most crop has several specific names called by each language group)	madua (*E. coracana*)/khadua (*E. indica*) gruji suau (*Echinochloa frumentacea*)/dhera (a weed, *E. colona*) merendo, kodowar (a mimic weed, *P. scrobiculatum*)/matwali, kharasami (a weed, *Paspalum sp.*)
2.	added a few adjective words	
2.1	meaning "weed"	lingudi (*Setaria pumila*)/ghas lingudi (the weed) kodo/kodo ghas,
2.2	like "another crop"	same melatti (a mimic weed, *B. ramosa*) [like little millet] akki hullu (a mimic weed, *P. sumatrense*) [weed like rice]
2.3	indicating a morphological trait	ragi kaddi (a weed, *E. indica*) [finger millet with spike like a stick] bilai lange (a weed, *S. pumila*) [cat's tail]
2.4	indicating an ecological trait	samulu (*Panicum sumatrense*)/yerri arasamulu (the weed with grain shattering) same (*P. sumatrense*)/samuru korra (*S. pumila*) [foxtail millet growing in little millet field] varagu sakkalathi (*S. pumila*) [a mimic weed, second wife of kodo millet] sakkalathi same (a mimic weed, B. ramosa) [second wife of little millet]
2.5	indicating a utility	same (*P. sumatrense*)/ pil same (*Brachiaria ramosa*) [for fodder],
IV	Classified into some landraces	marua (*E. coracana*): three varieties; agat- [early], madhyam-[medium] and pichhat-[late] /maruani (E. indica). sama (*P. sumatrense*): four varieties; manchi-[summer], pala-[short], ara-[tall] and varagu-[sowing in January].

Unknown (Stage I): farmers do not have specific names for wild or weedy plants, often referring to them genetically as *ghas* and *hullu.*

Non-distinctive (Stage II): the same name is used for both crop and weed forms, such as *ragi.*

Identified (Stage III): distinctions are made between domesticated and wild types; for example, domesticated *Eleusine coracana* is called *madua,* while wild *Eleusine indica* (weed) is referred to as *khadua*. Farmers may also use descriptive adjectives as the root of the millet name to highlight traits like weed status (*ghas lingudi* for *Setaria pumila*), mimicry (*same melatti*, meaning "mimic weed like little millet"), morphological features (*bilai lange*, meaning "cat's tail"), or ecological trait (*yerri arasamulu*, meaning "weed with grain shattering"), or utility (*pil sama*, meaning "*Brachiaria ramosa* for fodder").

Classified into local varieties (Stage IV): Millets are further subdivided into regional varieties. For instance, *Eleusine coracana* is called *marua* and divided into *agat-* (early), *madhyam-* (medium), and *pichhat-* (late) types, while the wild week *Eleusine indica* is known as *maruani*.

Thus, although naming conventions can differ regionally, farmers generally possess a nuanced understanding of millets and their relatives, distinguishing between crop types, wild forms, and utility-based varieties.

Domestication process of millets

More than 30 grass species have been domesticated as cereal crops in different regions worldwide. For example, *Hordeum vulgare* was domesticated approximately 12,000 years ago.

Despite their nutritional potential within native habitats, many of these species now face threats to their continued existence due to abandonment or limited cultivation. This decline is largely the result of major advances in crop improvement programs that have increased the yield and production of key cereals such as wheat, rice, and maize. Consequently, other grain crops, particularly millets, have gradually decreased over the previous century, leading to significant genetic erosion of local varieties. Recognizing the importance of these underutilized genetic resources is crucial, particularly given their adaptability to stress-prone environments. Most millet species are C_4 plants, notable for their early maturation and resilience in conditions of severe drought and intense sunlight.

Certain indigenous millet varieties continue to be cultivated by local farmers, providing essential material for research into crop evolution and the origins and dispersal routes of domesticated plants. In the Indian subcontinent, some small millets remain in the process of domestication (Kimata et al. 2000; Singh and Arora 1972). While botanical data are fundamental to reconstructing crop evolution, insights from local farmers regarding agricultural practices help clarify the geographical origins and dispersal patterns of these crops.

Vavilov (1926) described a domestication process in which weeds associated with wheat evolved into secondary crops within two genera, *Avena* and *Secale*. For example, *Secale cereale* L. developed substantial cold resistance in high-altitude and high-latitude regions, permitting cultivation under harsher conditions than wheat. Kobayashi (1987, 1989) proposed a model for the domestication of Indian millets as secondary crops that descended from weed companions of *Oryza sativa* L. The spread of O. *sativa* in the Indian subcontinent began in wetlands and then migrated to uplands, causing ancestral weedy plants to successively invade paddy and upland rice fields. Such species include *Panicum sumatrense* Roth. (little millet), *Paspalum scrobiculatum* L. (kodo millet), *Echinochloa frumentacea* Link (Indian barnyard millet), *Brachiaria ramosa* (L.) Stapf. (korne), *Digitaria crusiata* (Nees) A. Camus (raishan), and *Setaria pumila* (Poir.) Roem. & Schult. (korati; syn. *S. glauca* (L.) P. Beauv.) (Chandra and Koppar 1990; de Wet et al. 1983a, b, c). In particular, *Pas. scrobiculatum*, *P. sumatrense*, and *E. furumentacea* were domesticated as secondary crops as they demonstrated superior drought tolerance compared to upland rice in Eastern India, where several millet species were domesticated.

S. pumila is an annual weed that typically grow between 30 and 60 cm tall. Its inflorescence forms a cylindrical, densely flowered, spike-like raceme ranging from 2.5 to 10 cm in length. The predominant color is yellow, though purplish and pale green variations are also observed. This grass is fairly common in cultivated fields, along roadsides, and in cleared forests up to 700 m in elevation. The spikelets (c.a. 3 mm long) appear pale green or brownish-green, and the species is favored by livestock (Achariyar 1921; Singh 1988). As a polyploid plant (2n = 18, 36, 72), *S. pumila* has a largely unknown genome constitution and is closely related to genome D (Zhao et al. 2013).

The domestication process of *S. pumila* is proposed to occur in four distinct stages, as illustrated in Figure 41. Initially, the species transitioned from growing along roadsides and in unstable habitats to invading upland rice fields. The second stage saw *S. pumila* develop an agro-ecological niche for fodder use and establish itself as a companion weed in upland rice and millet fields. The third stage marked the shift from mimic companion weed to semi-domesticated insurance crop during times of famine, under mixed cropping with *P. scrobiculatum*, *E. coracana*, and *P. sumatrense*. After integrating into upland rice and millet fields and facing intensive weed control measures, these weeds evolved to mimic particular crops, forming complex weed–crop associations. Farmers moderated weed control practices during this stage. The fourth and final stage involved these mimic companion weeds being adopted as both a fodder source and supplementary grain.

Specifically, for *S. pumila*, reduced weeding in regions such as the Deccan provided crop insurance during extreme droughts, allowing the species to develop taller forms with larger spikes and seeds accompanied by less shattering, and gradually progressing toward domestication. Mimetic traits such as elongated leaves, fewer tillers, and increased height emerged in fields dominated by *P. sumatrense*, while anthocyanin pigmentation in leaves and sheaths assisted mimicry among grain crops and related weeds in mixed crop stands (Kimata 2015a, Kimata et al. 2000).

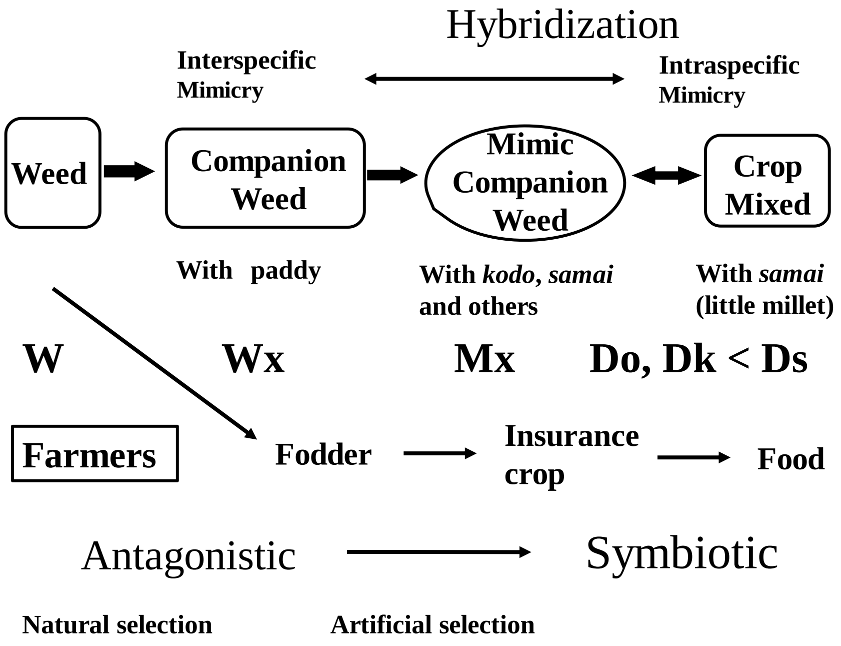


Figure 41. Domestication process of *S. pumila* in relation to the weed–crop complex.

S. pumila concurrently diversified its traits through hybridization among the four distinct types, driven by natural and artificial selection in severely arid environments. Companion weeds that mimicked crop species were harvested together with other (crop) millet varieties and unintentionally sown again the following season. Recently, this process has advanced to encompass mixed cropping practices. *S. pumila* is regarded as a “tertiary crop” in relation to its associated secondary crops, such as *P. sumatrense* and *Pas. scrobiculatum*, with respect to rice. The domestication of *S. pumila*, a tertiary crop mixed with other grain crops, proceeds from inter- and intraspecific mimicry by natural and artificial selection in sympatric fields. This evolutionary process is primarily attributed to adaptation to aridity, accompanying the spread of *S. pumila* from eastern to southern regions of the Indian subcontinent.

Archaeology of millets

Table 37, which draws from and updates Fuller et al. (2001), documents the earliest appearances of grain crops in South Asia (Fuller and Madella 2001; Fuller, personal communication). During the Early Phase of Harappan sites (around 4500 B.C.), remains of *H. vulgare*, various *Triticum* species, and a few *Avena sativa* were recorded. The Mature Phase (around 2600 B.C.) saw the introduction of numerous *O. sativa* samples and a few instances of *Panicum miliaceum*. By the Late Phase (around 2000 B.C.), there was a notable increase in *Setaria* species, several findings of *Sorghum bicolor*, and limited occurrences of *Pennisetum glaucum* (syn. a*mericanum*, trace).

In early South Indian sites (2300 to 1800 B.C.), archaeobotanical investigations uncovered traces of *Panicum sumatrense*, abundant remains of *Brachiaria ramosa* and *Setaria verticillata*, as well as trace amounts of *S*etaria *pumila*. Later sites, spanning from 1800 to 1200 B.C., revealed traces of *Paspalum scrobiculatum* and frequent evidence of *Echinochloa* cf *colona*, which may represent *Echinochloa frumentacea*.

Historically, Asian millets emerged in the following order: *Panicum miliaceum* was the first to appear, succeeded by *Setaria* species. These were followed by *Brachiaria ramosa*, *Setaria verticillata*, *Panicum sumatrense*, and *Setaria pumila*. The appearance of *Echinochloa* cf *colona* and *Paspalum scrobiculatum* occurred at a later stage. It is plausible that certain species, including *Brachiaria ramosa*, *Setaria verticillata*, *Setaria pumila*, and *Echinochloa* cf *colona*, were initially collected as wild grains before their domestication.

Recent archeological research has provided significant insights into the history of millets in the Indian subcontinent. Excavations have revealed millet grass remains in layers dating to the Southern Neolithic Phases II (2300–1800 cal. BC) and III (1800–1200 cal. BC). These remains primarily include browntop millet (*Brachiaria ramosa*) and bristly foxtail millet-grass (*Setaria vercillata*), with small quantities of yellow foxtail millet (*Setaria pumila*) also detected, likely gathered from wild stands (Fuller et al. 2001).

In the context of the Harrappan Civilization, the earliest cereals cultivated during the Early phase (before 2600 BC) were wheat, barley, and oats. The Mature phase (2600–2000 BC) saw the introduction of *Eleusine* species (problematic, *E. coracana*), *Setaria* species, and *Panicum* species. In the Late phase (post-2000 BC), additional crops such as *Paspalum*., *Echinochloa*, *Sorghum*, and *Pennisetum* species joined the agricultural systems (Fuller and Madella 2000; Weber 1992).

Table 37. Summary on the first occurrence of grain crops in South Asia

Species	Early	Mature	Late		(South India)			
Period	4500 B.C.-	-2600 B.C.	-2000 B.C.	2300-1800 B.C.	1800-1200 B.C.	-0 A.D.	1500 A.D.	1900 A.D.
Paspalum scrobiculatum					trace			
Panicum sumatrense				trace	a few			
Echinochloa cf. colona					many			
Brachiaria ramosa			wild?	many	many			
Setaria verticillata			wild?	many	many			
Setaria pumila			wild?	trace	trace			
Setaria sp.			a great many					
Digitaria cruciata								domesticated
Digitaria sanguinalis							(unknown, disapeared)	
Panicum miliaceum		a few						
Panicum sp.			a few					
Setaria italica			possible					
Eleusine coracana			?	possible				
Sorghum bicolor			many					
Pennisetum glaucum			trace	trace	trace			
Coix lacryma-jobi						possible		
Oriza sativa		many		trace	trace			
Hordeum vulgare	a great many			many	many			
Triticum dicoccum				trace	trace			
Triticum durum/aestivum				many	trace			
Triticum sp.	a great many			many	many			
Avena sativa	a few							
Zea mays							introduced	

Modified and Based on Fuller et al. 2001, Fuller and Madella 2001, and Fuller (personal communication).

Dispersal routes of millets in the Indian subcontinent

The domestication and dispersal routes of several Indian millet species have been systematically investigated, revealing distinct patterns for each crop.

Kodora, *Paspalum scrobiculatum*, was domesticated in approximately 2000 BC in India. This species is cultivated throughout the Indian subcontinent, with primary distribution in Madhya Pradesh. Comparative studies involving 32 accessions, including weed forms, have been conducted. The relationship between plant pigmentation and rice mimicry was observed in 16 accessions, including six collected from upland rice fields. The domestication of kodora as a secondary crop to upland rice involved a transition from perennial to annual life cycles and the acquisition of crop-like features through interactions with rice cultivation (Ishikawa unpublished). Genetic analyses (AFLP and chloroplast trnK/matK region sequencing) identified two groups among cultivated accessions: one northern and genetically similar to weed forms from upland rice fields in Orissa; and one southern, related to upland rice field accessions in Orissa and weed types in southern states.

Two hypotheses regarding the origin of *Paspalum scrobiculatum* were proposed: (1) kodo millet was domesticated once in Orissa and then diffused to inland and southern states; (2) kodo millet was domesticated in Orissa and southern India independently (Ishikawa 2007).

Jangora (Echinochloa furumentacea) is cultivated for food, fodder, and emergency use in India, Nepal, and Pakistan. Its ancestor, *Echinochloa colona*, is a common weed in paddy fields. Morphological and AFLP analyses of seven accessions of *Echinochloa colona* and 42 *Echinochloa furumentacea* accessions suggest that Bihar is the likely origin, with subsequent spread to Tamil Nadu via Karnataka (Kagami unpublished).

Samai (Panicum sumatrense), is cultivated for food and fodder in India, Nepal, Sri Lanka, and

Myanmar. Its ancestral form, *Panicum sumatrense* subsp. *psilopodium*, also occurs in paddy fields. Morphological and AFLP analyses of 38 accessions and 281 herbarium specimens indicate Eastern India as the origin, with subsequent dispersal to Southern India (Otsuka unpublished).

Korne (*Brachiaria ramose)* is primarily grown as food crop through extensive farming in only India. Its ancestor is a weed found in paddy fields. Morphological and AFLP analyses of 70 accessions, encompassing weed and domesticated types collected in Pakistan and India suggest that southern Orissa is the origin, with further spread across the Deccan Plateau via Tamil Nadu (Otsubo unpublished).

Korati (*Setaria pumila*), a cosmopolitan weed, is primarily found in mixed cropping systems with *Paspalum scrobiculatum* or *Panicum sumatrense* in India (Kimata et al. 2000).

The integrating hypothesis for millet dispersal in India, as illustrated in Figure 42, suggest that *Echinochloa furumentacea*, *Panicum sumatrense*, and *Paspalum scurobiculatum* originated as secondary crops associated with upland rice. Initially, their ancestral plants were companion weeds derived from the relative weeds that invaded paddy fields in humid regions of Eastern India. Subsequently, the companion weeds became insurance crops in upland rice fields and spread to a dry region in the Deccan Plateau (Kobayashi 1987, 1989). *Brachiaria ramosa* and *Setaria pumila* ae classified as "tertiary crops," domesticated from related weeds in upland millet fields. In contrast, *Digitaria cruciata* has recently emerged from a related weed in maize or vegetable fields in Kashi Hill, Meghalaya, and remains geographically restricted (Singh and Arora 1972).

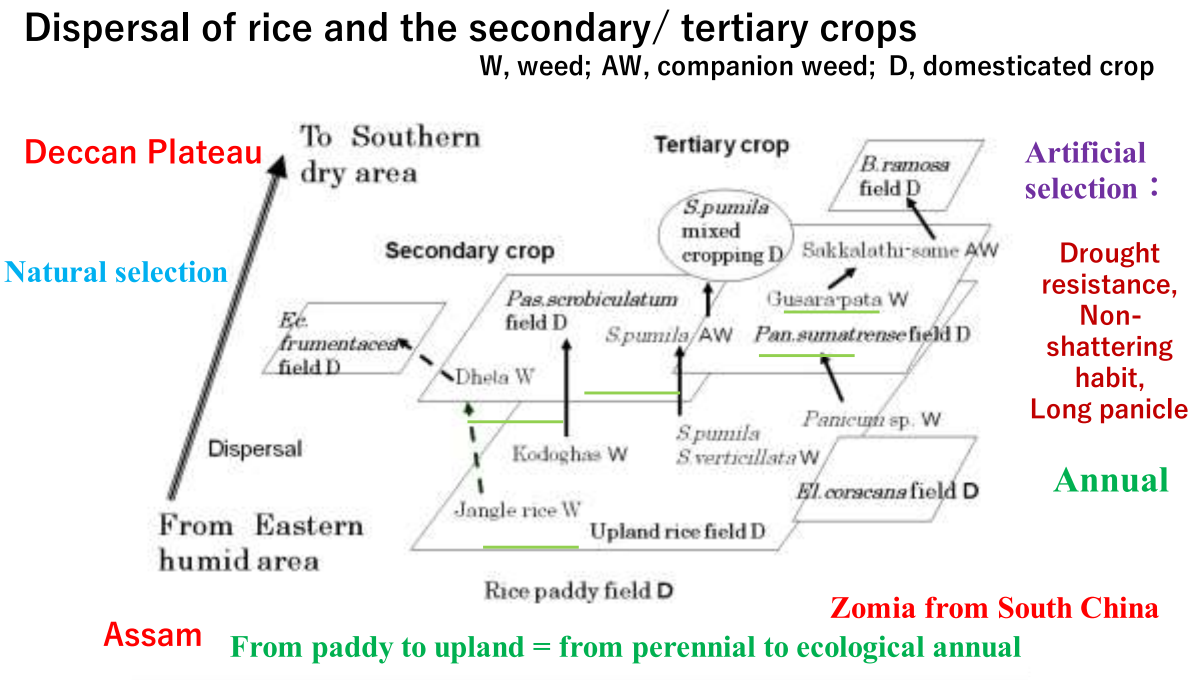


Figure 42. Domestication process of millets in the Indian subcontinent

In summary, the domestication of Indian millet species followed a diffusion trajectory that began in the humid paddy fields of Eastern India and extended to the arid upland rice fields of the Deccan Plateau in Southern India. This process, supported by archaeological, field (Kimata et al. 2000), experimental (Kimata 2015a, 2015b), and linguistic data, primarily occurred in the Eastern

Ghats and Southern Deccan Plateau (Figure 42). The concept of secondary origin via weed and mimic weed types clarifies the complex millet domestication process. Much like oats and rye became cold-tolerant wheat companions (Vavilov 1926), Indian millets emerged as drought-tolerant secondary crops alongside upland rice. *Bachiaria ramosa* developed greater drought tolerance than *Setaria pumila*, becoming an independent crop, while both are considered tertiary crops due to their double secondary status with other millets and upland rice. Millet domestication underscores the importance of weed–crop complexes and basic agricultural complexes in plant–human coevolution.

Chapter 6 Food processing and cooking methods of seed grains

Cereals, including millets, have served as staple foods throughout Eurasia since ancient times. Among millets, common (proso) and foxtail millets were cultivated in areas covering almost the whole of Eurasia. Archaeological evidence suggests these two crops were staple foods of both the Neolithic Yan-Shao people of North China and residents of Neolithic European villages during the fourth millennium B.C. (or 8500 B.P.; Jones 2004). These grains spread from their regions of domestication across Eurasia in prehistoric and historic eras. Human ancestors developed cultural diversity grounded in Earth's natural diversity. Civilization's foundations rest on agricultural culture complex—fundamental aspects of society—with millet processing and cooking as essential elements alongside farming practices. Thus, the botanical studies of domestication are enriched by comparative study on processing and cooking methods, clarifying the geographical origins and dispersal of different millets (Kimata and Seetharam 1997).

Japanese cuisine developed under the influence of Chinese, Indian, and African agricultural traditions. Many foundational techniques for processing and cooking millets are incorporated into Japanese grain preparation, and millets remain important crops in semi-arid and mountainous regions, including Japan, for future utilization.

Generally, cereal grain uses fall into two categories: foods and drinks. Food uses break down further into preparation of whole grain, meal or flour; drinks include non-alcoholic and alcoholic varieties. Since antiquity, common and foxtail millets have been used extensively for traditional foods and beverages across Eurasia. In East Asia, dishes such as boiled grain, gruel, *mochi* (in Japanese), and alcoholic drinks are popular, while Southeast Asia and Europe favor meal porridge, bread, and non-alcoholic drinks.

The main processing methods are outlined in Figure 43. Once our ancestors harnessed fire, civilization progressed rapidly. Wrangham (2009) summarized this development as follows: C. Darwin cooked with hot rocks in earth ovens and called fire-making "probably the greatest [discovery], excepting language, ever made by man," acknowledging the value of cooked food but not its evolutionary significance. Darwin thought fire was irrelevant to how we evolved. Most anthropologists followed Darwin's view that cooking was a late addition to the human skill set with no biological or evolutionary significance.

A century later, cultural and elite anthropologist C.L. Lévi-Strauss's analysis reinformed this notion, which has remained largely unchallenged. Indeed, his implication that cooking had no biological meaning was widely touted. Conversely, French gastronomist J-A Brillat-Savarin wrote in 1825 that "It is by fire that man has tamed Nature itself," arguing that after humans began cooking, meat became more desirable, boosting hunting's prominence. Cooked offers many benefits: it enhances food safety, creates rich flavors, reduces spoilage, and makes tough foods easier to process. However, the most crucial, though often overlooked, advantage is that cooking increases the energy our bodies extract from food. Humanity, in many ways, is shaped cooks, we rely on a diet adapted to cooked food, influencing our body and minds.

This theory proposed by Wrangham (2009) extends to cereals as well as meat. Nakao (1972) noted that research on processing and cooking had been limited, which puzzled him given these practices' importance in agricultural culture complexes. Countless cooks worldwide have developed diverse and delicious recipes, yet the fundamental, early methods—central to agricultural culture—remain especially intriguing, as suggested by Nakao's hypotheses (1967, 1972). Nakao (1972) believed rice was first domesticated in eastern India; however, generic analyses (Xuehui Huang *et al*. 2012) reveal rice's domestication occurred around the Peal River in south China. Therefore, Nakao's otherwise insightful theory regarding agricultural culture, especially the spread of processing and cooking methods, warrants reconsideration. This new understanding significantly alters views on rice and the associated secondary Indian millets.

Processing methods of seed grains

There are two strategies for millet processing: parboiling and wet milling. In Japan, grains such as Japanese barnyard millet are parboiled prior to de-husking, while in India, this technique is applied to grains like little millet. Parboiling facilities the efficient removal of husks from small millet grains. Subsequently, flour produced through wet milling is used for consumption and as offering in religious contexts in Japan and India. This underscores the cultural significance of certain millets, which are accorded a status comparable to that of rice in both regions.

Two primary methods are used in milling process: dry and wet milling. Most grains are made into flour through dry milling; wet milling method is adopted to prepare flour.

The dissemination of millet-based cuisine involved not only the spread of millet cultivars (seeds) but also their cultivation, food processing, and associated tools and techniques. In traditional food processing, both parboiling and wet milling (known as *shitogi* in Japanese) are important in understanding the historical link between processing method and domestication. The parboiling method is considered one of the oldest processing techniques of millets and rice grains.

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Processing methods of seed grains

Bake; barley, rice, maize
Pop; common millet, rice, maize, amaranths
Roast; barley, adlay,
Parboil; Japanese barnyard millet, rice (*chiura*)

Heating

Crush; barley (*warimugi*)
Pound (polish) ; cereals
Dry milling; wheat, barley and so on
Wet milling (shitogi) ; foxtail millet, Japanese barnyard millet, common millet, rice, kodra
Soak; acorn, conker, kudzu vine, etc.

Coarsely ground
Polish
Milling
Clean water

Boil (grain); rice, barley, foxtail millet, Japanese barnyard millet, common millet, etc.
Steam (grain); rice, foxtail millet, common millet: (flour) wheat
Roast; rice, barley
Knead; finger millet, buckwheat, wheat, etc.
Bake (flour); rice, wheat, buckwheat
Pound (grain); rice, foxtail millet, common millet, sorghum, etc.

Boiled water
Heating

Germination (malt); barley, finger millet
Fermentation ; rice, barley, etc.

Alcoholic fermentation

Figure 43. Basic processing methods of seed grains

Wet milling method and flour foods

During the *Jomon* period in Japan, people gathered various nuts, such as *Quercus serrata* (Figure 44a), *Castanopsis sieboldii* (Figure 44b), and *Castanea crenata*. Since these nuts were generally bitter, water from the stream was used to removed bitterness and make flour using the water bleaching method. Moreover, flour was collected from *Dioscorea* spp., taro, and sago palm, among other places (Nakao 1967). *Jomon* people had become easily to get much food materials, and then they had obtained their stable life. This water bleaching method might have influenced wet milling methods of seed grains, such as *shitogi* (Figures 45 and 46).

Figure 44. Nuts, parched grains and barley/wheat fields

a, *Quercus serrata*; b, raw edible nut, *Castanopsis sieboldii*; c, roasted rice; d,e, roasted barley; f, barley fields; g, wheat field mixed with many kinds of weed at the Botanical Garden of Free University of Berlin.

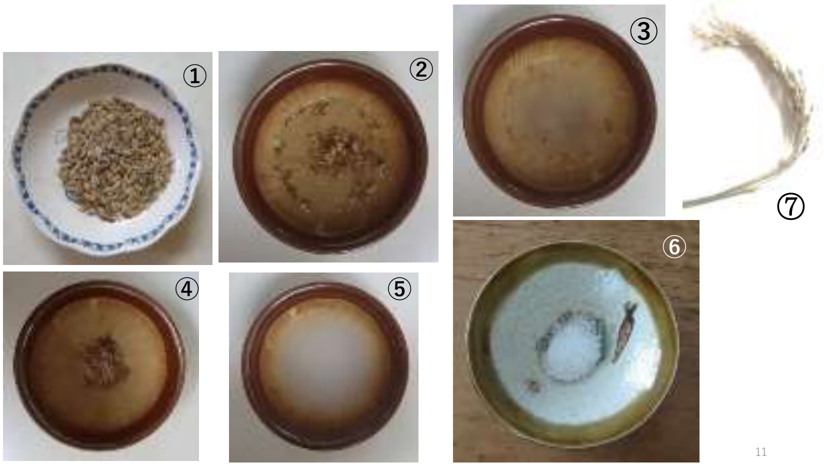

Figure 45. Wet milling method, *shitogi*

① Upland rice grains; ② soaking; ③④⑤ pounding and removing hull; ⑥ drying *shitogi* flour; ⑦ panicle of upland rice.

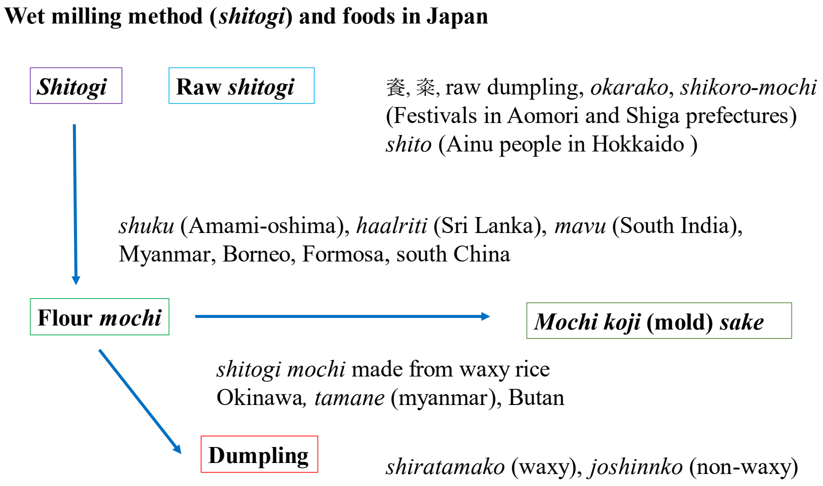

Figure 46. Wet milling method (*shitogi*) and foods in Japan

Kona-mochi (flour) and *Koji-sake* originated from *shitogi* (Figure 46). The Ainu people prepared *shito* from millet to offer their god *Kamui* (Figures 47 and 48). Similar foods are known as *shitogi* in Aomori, *shuku* in Amami-oshima, Kagoshima, *shutonpa* made by children at koshiki-jima and generally *nama-dango*, *okarako,* or *shikoro-mochi* (raw dumpling for offering to gods). Villagers used *shitogi* (raw rice flour) during festivities.

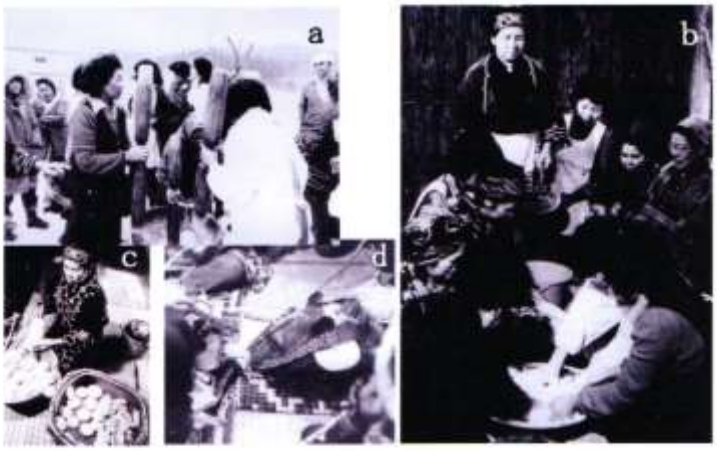

Figure 47. Ainu people making *shito* from foxtail millet and common millet

a, Pounding polished grains by mortar and vertical pestle; b, kneading flour by hand; c, shaping in discs; d, offer *shito* to gods *Kamui* through a bear which is the messenger (Photographs permitted by Kaizawa.)

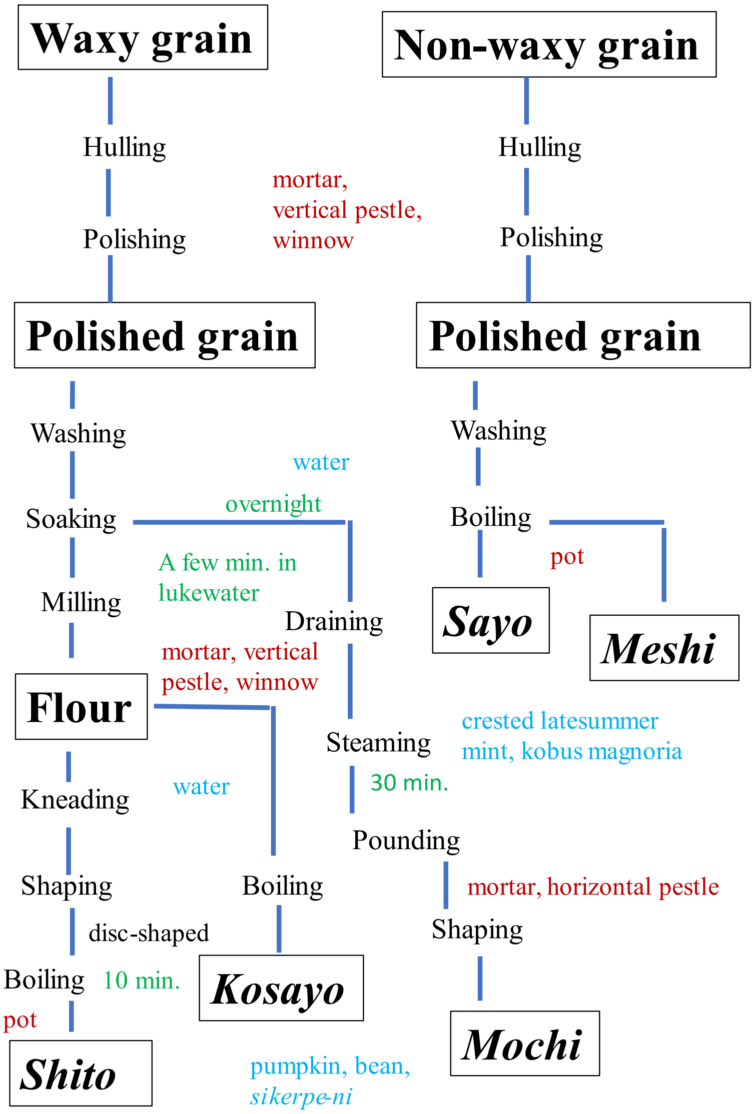

Figure 48. Cooking methods of foxtail millet in Saru river bioregion, Hokkaido

Shitogi was made from Japanese barnyard, foxtail, and common millets, as well as rice. Ainu people grew two varieties of Japanese barnyard millet: *Ainu-bie* and *Nanbu-bie* (Figure 49).

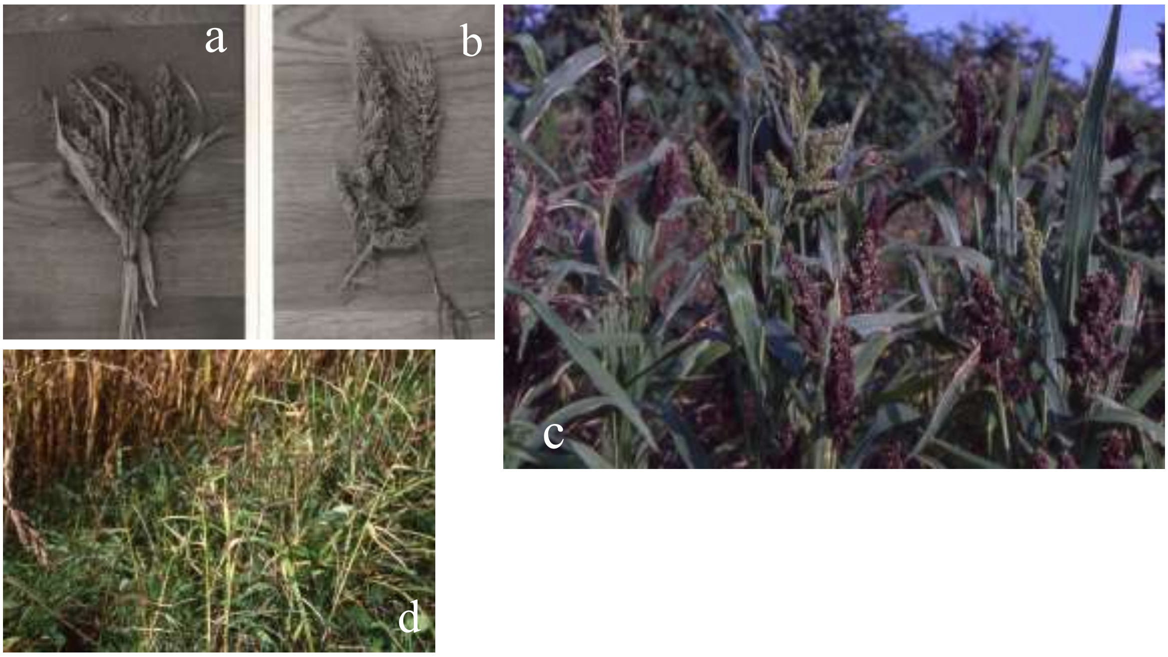

Figure 49. Japanese barnyard millet, *Echinochloa utilis* in Hokkaido, Japan
a, *Nanbu bie*; b, *Ainu bie*; c, *Nanbu bie* on a farm; d, *Echinochloa crus-galli* on a levee of paddy field.

Nakao (1972) had not observed a food similar to *shitogi* in India. However, *mavu*, a dish in Tamil Nadu, India, consists of raw flour ball mixed with sugar and honey, and is closely resemble *shitogi* from Japan (Figure 50). *Mavu* is made from the flour of foxtail millet in several villages in Tamil Nadu (Table 38) and is offered to gods and goddesses before being eaten by locals. *Pidimavu* is made from rice flour mixed with *ghee* and is another a kind of taper offered to the gods and goddesses. These raw flours are produced through traditional wet milling techniques using a pounding mortar, common for processing Asian millets and rice. Such raw flour foods are found in South India, Sri Lanka, Myanmar, Thailand, Laos, Kalimantan, Formosa, South China, and Japan.

For example, in Tamil Nadu, *mavu* (syn. *shitogi*) is made from foxtail millet (*S. italica*) and rice (*O. sativa*) as offering gods and goddesses. This wet milling method used here is notable when compared to the raw *shitogi* made from rice and some Asian millets in Japan. Additionally, this rice flour is frequently cooked into *bonda*, a fried snack in India.

Figure 50. Wet milling method of rice (same foods as *shitogi* in Japanese) in Andhra Pradesh
a, pounding rice grains; b, soaking grains in water; c, drying and filtering; d, *pidimavu*, a type light offered for gods and goddess.

Table 38. Cereal ingredients and their cooking styles in Tami Nadu

Material/Cooking	sadamu	uppuma	chapathy	roti	nan	poori	vadai	dosai	idlai	kali	kulu	mavu	Total
Brachiaria sp.													0
Ec. frumentacea	○	△					○			○	○		5
El. coracana	△	○		○			□	○		□	○		7
H. vulgare		○		○				○	□	○	○		6
O. sativa	□	○					○	○		○		△	6
Pan. miliaceum	○	△					△			○	○		5
Pan. sumatrense	○	○					○	○		○	○		6
Pas. scrobiculatum	○									○	○		3
Pe. americanum	○			△						○	△		4
Se. italica	○	△					○	○		○	○	○	7
Se. pumila													0
So. bicolor	○	△		△			○	△		○	○		7
T. aestivum			○					○		○	○		4
T. dicoccum		○											1
T. durum		△	△			△							3
Z. mays		○					△			△	○		4
Total	9	11	2	4	0	1	8	7	1	12	11	2	68

Grain foods and parboiling method

The parboiling method is one of the oldest grain processing techniques for millet and rice grains. In eastern India, most Indian millets and upland rice are frequently parboiled (Kimata and Sakamoto 1992), while nearly all millets are parboiled prior to consumption in Bangladesh. Notably, the practice of parboiling developed and continues to be used in regions extending from India to Myanmar for domesticated varieties in Indian millets and rice (Islam 1993; Muller 1988). Approximately half of rice produced in India is produced using the parboiling technique. In western Africa, this method is also used to produce rice.

Parboiling imparts several benefits to grains. First, parboiled grains are protected from pests and molds, enabling extended storage and timely consumptions. Second, parboiling allows unripe grains harvested prematurely to harden adequately, facilitating hulling and polishing (Nakao 1967). This method might have been develop to address the shattering of crop grains, which is common at the early stages of domestication, necessitating harvest full ripening. The application of this technique likely increased the yield collected by early agriculturalists. Following parboiling treatment in Japan, the glumes, lemmas, and paleas of *Echinochloa utilis* can be easily removed (Yabuno 1987), and similar advantages apply to *E. furumentacea* and *Pas. scrobiculatum*, which possess multi-layer hulls (Malleshi and Hadiwani 1993).

Third, parboiling facilitates nutrients transfer from the pericarp-testa into the endosperm and converts starch from its raw states to pregelatinized form, enhancing the nutritional value, flavor, cooking properties of polished grains (Achaya 1984, FAO1985, Malleshi 1989, Muller 1988). During parboiling, a layer of gelatinized starch is formed on the grain's surface, preventing the nutrient leaching during boiling, which is a significant advantage in India, since boiled grain is cooked usually with the "draining off" method and nutrients are discarded with the excess boiling water.

This process confers several benefits: 1) Hardened unripe grains enable easier dehusking and polishing when harvested early to prevent shattering (Nakao 1967). In Japan, parboiling of Japanese barnyard millet can easily remove the glumes, lemmas, and paleas (Yabuno 1987). 2) The nutrients contained in the seed coat permeate into the endosperm, the starch changes from a raw to pregelatinized form, significantly improving the nutritive value, taste, and ease of preparation of polished grains (nutritive value, taste and easy cooking) (Malleshi 1989). 3) The grains are protected from pests and mold, enabling proper storage and timely consumption.

The parboiled method is often used to process the Indian millets and upland rice, particularly in East India (Table 39, Figures 51, 52 and 53). Conversely, the other cereals, including African millets, wheat, barley and maize require no parboiling since most have naked grains except for the covered cultivars of barley. Notably, the parboiled method within the domesticated regions of Indian millets and rice

Table 39. Number of cases processed by parboiled method in the survey of India (1985, 1987, 1989)

Species	Maharashutra	Madhya Pradesh	Maharashutra	Karnataka	Tamil Nadu	Andhra Pradesh	Orissa	Bihar	Total
Pan. miliaceum								4	4
Se. italica									0
Brachiaria ramosa									0
Ec. frumentacea							1	1	2
Pan. sumatrense				1	1		3	4	9
Pas. scrobiculatum				1			3	1	5
Se. pumila							1		1
O. sativa				2	2	1	3	7	15
El. coracana									0
Pe. americanum									0
So. bicolor									0
H. vulgare									0
T. aestivum									0
T. dicoccum									0
T. durum									0
Z. mays									0
Total	0	0	0	4	3	1	11	17	36

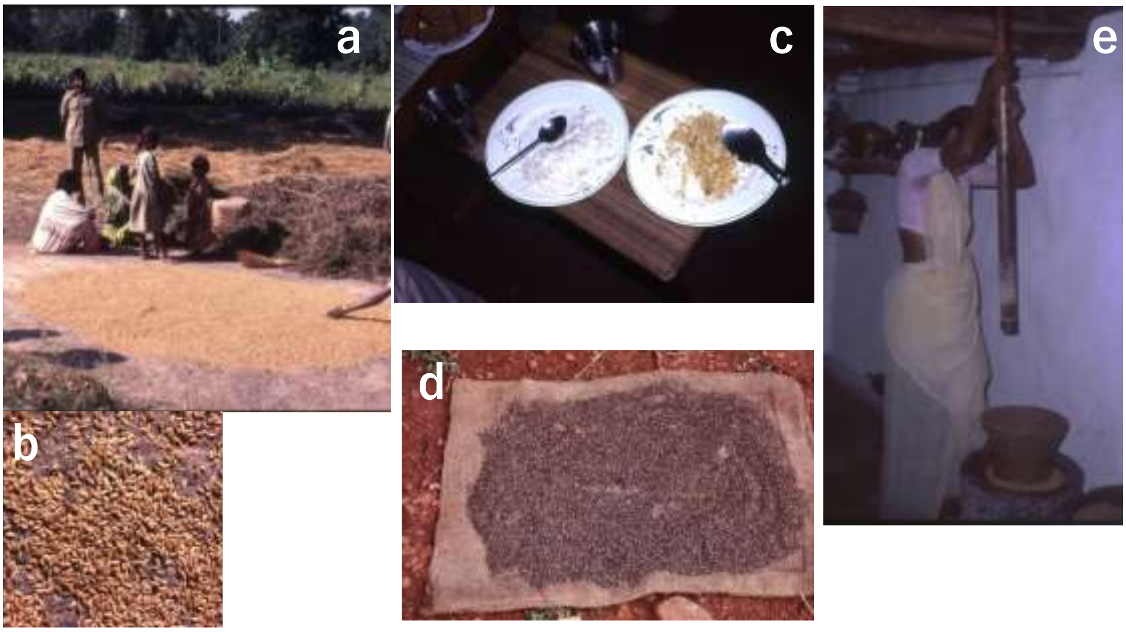

Figure 51. Parboiling method

a,b, Drying rice grains after boiling; c, *chiura*; d, drying *samai* grains after boiling; e, mortar and pestle for pounding foxtail millet.

Figure 52. Black steaming method of Japanese barnyard millet in Japan

Unhulled rice grains
Soaking for 2~3 days
Boiling for a few min.
Draining hot water
Roasting grains in iron pot
Pounding the broken grains by motor
Winnowing for remove their husks
Chiura, beaten rice

Figure 53. Chiura in India

Table 40 shows how parboiling affects dehulling. Ketto TR200 could dehull *S. italica* and upland rice. Since *E. utilis*, *P. miliaceum*, *Pas. scrobiculatum,* and *S. pumila* have a very smooth glume and lemma, TR200 could not dehull them; however, Ketto Pearlest was attempted. Parboiled unripe and ripened grains of *S. italica* and parboiled unripe upland rice grains were easier to dehulled than other batches of other millets and upland rice. The physical benefit of parboiling was most apparent with *S. italica*, as both parboiled unripe and ripened grains had much lower rations of broken grain after dehulling process by TR200 were considerably lower than those of non-parboiled ones. In contrast, for other species, parboiled grains tended to break more easily or showed no significant difference between batches, especially when using Pearlest. The TR200 dehulls similarly to traditional mortar used by farmers, whereas Pearlest's gentler grinding helps prevent grains breakage. Therefore, parboiling effects unripe and ripened grains of *S. italica*, and ripened upland rice grains and should be performed to prevent the shattering in ripened grains of these species. However, *S. italica* has not been traditionally parboiled, whereas *Pas. scrobiculatum* has in eastern India, as *E. utilis* has done in Japan (Kimata, M., S. Fuke, and A. Seetharam 1999).

Table 40. Effect of parboiling on the dehulling and polishing of millet grains (20 g grains)

Species	Hulled grains	Broken grains	Hulls	Grains with hull
Lot	(g)	(g)	(g)	(g)
TR200				
Setaria italica				
unripe grain	11.14	5.30	2.11	1.48
ripen grain	12.06	4.24	2.80	0
unripen grain parboiled	15.90	1.26	2.83	0
ripen grain parbouled	15.34	1.78	2.89	0
Echinochloa utilis				
unripen grain parboiled	0.14	0.79	1.22	17.85
ripen grain parbouled	0.05	0.86	0.59	18.50
Paspalum scrobiculatum				
ripen grain	2.56	3.40	4.43	9.61
ripen grain parboiled	2.16	4.34	3.61	9.89
Setaria pumila				
ripen grain	2.55	7.17	7.31	2.97
ripen grain parboiled	1.78	9.62	6.48	2.13
Oryza sativa				
unripen grain	11.08	1.54	4.42	2.95
ripen grain	13.37	0.39	3.63	2.61
unripen grain parboiled	12.66	1.12	4.34	1.88
ripen grain parboiled	13.12	0.64	3.58	2.44
Pearlest				
Panicum miliaceum				
unripen grain	15.77	0.13	4.11	not tested
ripen grain	15.52	0.28	4.29	
unripen grain parboiled	15.01	0.40	4.59	
ripen grain parboiled	15.10	0.18	4.71	
Echinochloa utilis				
unripen grain	14.32	0.12	5.56	
ripen grain	14.85	0.21	4.94	
unripen grain parboiled	14.38	0.12	5.51	
ripen grain parboiled	14.97	0.10	4.94	
Paspalum scrobiculatum				
unripen grain	13.04	0.04	6.93	
ripen grain parboiled	13.22	0.06	6.73	
Setaria italica				
unripen grain	11.96	0.29	7.75	
ripen grain parboiled	11.97	0.32	7.71	

The protein contents (expressed as a percentage (%)) in grains from five millets and upland rice, following dehulling or polishing, are summarized in Table 41. Grains of *E. utilis*, *Pan. miliaceum,* and *S. pumila* contain protein levels exceeding 11% of their dry weight, whereas *S. italica*, *Pas. Scrobiculatum,* and upland rice contain approximately 7%. Parboiling increases the protein content of unripe and ripe grains of *S. italica*, and significantly decreases that of *S. pumila*. Conversely, parboiling exerts an insignificant effect on the protein contents of unripe grains in *E. utilis* and *Pan. miliaceum*, but somewhat decreases that in ripened grains. Parboiling also had a minimal effect on the protein contents in *Pas. scrobiculatum* and upland rice. These results indicate that parboiling has no positive effect on the protein contents of millets and upland rice, except for *S. italica*.

Meanwhile, parboiling increases the free amino acid contents in unripe grain of *S. italica* and ripened grains of rice, as well as adenine nucleotide contents in unripe grains of *S. italica*, *Echinochloa utilis,* and *Panicum miliaceum*, and ripened grains *Paspalum scrobiculatum* and *S. pumila* (syn. *S. glauca*). Nonetheless, parboiling was not found to have a definitive effect on the nutritive value or amino acid composition of grain proteins.

Table 41. Protein content (%)* of samples used

Species	non-parboiled grains				parboiled grains			
	unripe		ripen		unripe		ripen	
	hulled	polished	hulled	polished	hulled	polished	hulled	polished
Setaria italica	6.88	6.56	7.75	7.69	11.25	10.75	8.94	8.63
Echinochloa utilis	14.88	14.31	18.63	16.88	14.88	14.63	15.56	14.81
Panicum miliaceum	11.69	11.5	13.69	13.63	12.19	11.50	11.88	11.69
Paspalum scrobiculatum	not tested	not tested	7.44	7.38	not tested	not tested	8.00	8.00
Setaria pumila	not tested	not tested	13.13	12.19	not tested	not tested	6.63	6.38
Oryza sativa	6.75	6.69	7.19	6.88	6.56	6.25	7.44	7.31

* (N x 6.25) on dry basis.

Heating grains

Beaten rice (*chiura*, *chura*, *aval*) is valued for being thin, papery, crisp, broad in shape, and as white as possible. To make it, first, paddy is soaked in water for 2 or 3 days until if softens. The same water is then briefly boiled and cooled. The swollen grains are heated in a concave iron or earthenware pan over high heat till they burst, after which they are pounded with a pestle to flatten them and remove the husk, which is followed by winnowing (Figures 51 and 53) (Nakao 1972, Achaya 1984). Nakao (1972) reported that *yakigome* is the same food as *chiura*, but prepared differently, involving boiling and parching (Kimata 1991, Nakao 1972). Nakao also suggested that this method was once dispersed from India to Japan in ancient times and disappeared in disappeared from the regions in between, so it became isolated in both countries.

However, I believe these methods originated independently in Japan (Figure 44cde), and *yakigome* had not spread from India. For example, popcorn has been a traditional food for the Native American since 3600 BC. Although basic cooking methods began independently in many places, similar combined methods became part of agricultural complexes during crop domestication and then spread centrally from the original area via human migration.

Parched paddy (puffed rice, *muri* or *murmura*) is produced as follow: Parboiled rice is preferred for puffing, and handfuls is tossed into very hot sand held in *kadai* over the fire. The sand is stirred with a metal ladle, and once the rice swell and crack, the mixture is poured into a sieve, the puffed rice is collected, and the hot sand reused. Rice soaked in or roasted with salt water is used for parching in eastern India (Figures 54 and 55ac). Commercial units with roasting cylinders are now commonly in operation. Through them, rice travels in hot sand and then sieved through and passes back into the cylinder. Ideally, puffed rice is expected to be white, glossy, and plump (Achaya 1984). Japanese children call it *pakkan* or *ponsen*.

According to Ayurvedic classics, *laja* (parched paddy) is a soft, light, whitish, commonly edible food product prepared by roasting paddy, has *deepan*, *laghu*, *grahi*, *snneha*, *kapha-meda-chedak*, *balya*, *rasayan* and *ojo-vardhak* properties and is uses as a remedy for *chardi*. Its classical uses, methods of preparation, differences from parched rice, changes in nutritional value during parching, and its future research aspect, have been well documented (Awantika, J. et al. 2015).

Wheat broken during threshing, known as *dalia*, is cooked as type of porridge. Like rice, wheat can also be puffed; the resulting friable product can be ground into a flour called *sattu.* Since it is precooked, *sattu* can be used to prepare various foods (Figures 54 and 55).

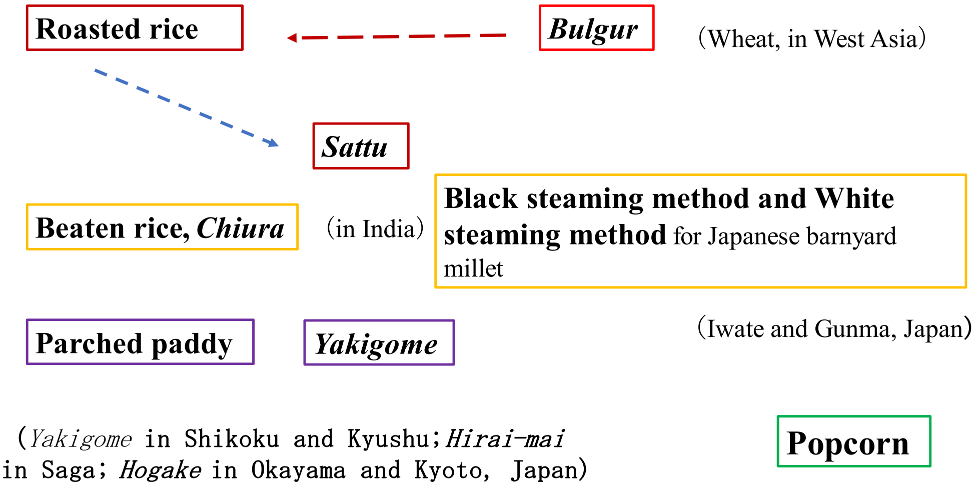

Figure 54. Heating grains by roasting, boiling, and parching

Figure 55. Parched grain of common millet

a, Thrown into very hot sand held in *kadai*; b, *upitu*; c, parched rice grain.

Indian food culture

Indian cuisine reflects the rich heritage of its people, embodying India’s historical evolution, religious beliefs, cultural practices, and geographical diversity (Sahni 1986). Across the Indian subcontinent, staple foods made from grains are often paired with various spicy curries and legume *dal* stews (*dhal*). Distinct regional cooking techniques are used for each type of cereal (Aziz 1983, Sahni 1986). Cereal preparation plays a vital role within the agricultural culture complex (Maheshwari 1987, Sakamoto 1988).

Several millets species have served as staple foods across Eurasia since ancient times. Among them, *Panicum miliaceum* and *Setaria italica* are cultivated in areas throughout much of Eurasia. Archaeological findings indicate that these two millets are used as staple foods for Neolithic Yan-Shao people of North China and cultivated in Neolithic villages all over Europe through the fourth millennium BC (Sakamoto 1987a, 1987b).

Foods made using millets

Various dishes featuring millets and cereals have been developed. Common preparations include *bhat* (*meshi* in Japanese), *roti* (*pan*), and *mude* (*oneri*); these dishes are made from most of the cereals listed in Table 42 (Kimata 1987). *Bhat*, the most popular food, is a boiled grain recipe prepared with all ingredients shown in Figure 59ad. *Bhat* origins trace back to ancient China, later spreading to the Indian subcontinent via Eastern India. *Roti*, another popular food made from cereal flour, originated from wheat breadmaking in the Fertile Crescent and entered the subcontinent by way of Western India. *Mude*, a popular food made from cereal flour, evolved from the Eastern Africa dish *ugari* arrived through the Arabian Peninsula. Figure 59 illustrates traditional methods for cooking cereals in the Indian subcontinent: (a) a traditional boiled rice with *papad* (crispy salted wafer made from *dal,* vegetables, and cereals); (b) *upma* and *khesari bhat*; (c) *dosa*; (d) *mude* and boiled grain made using *Brachiaria ramosa*; (e) *puli*; (f) *idli.*

Table 42. Millets and their food in the Indian subcontinent

Species name		Food								
	Indian name	bhat	upuma	roti	vada	dosa	idoli	mudde	ganji	mave
	Japanese name	meshi		pan	age pan		mushipan	oneri	konagayu	shitogi
Sorghum bicolor		○	○	◎	○	△	○	○	○	
Pennisetum americanum		○	○	◎				○	○	
Eleusine coracana		△	○	○	○	○	○	◎	○	
Setaria italica		◎	△	△	○	○		○	○	○
Panicum miliaceum		◎	△	○	△			○	○	
Panicum sumatrense		◎	○	△	○	○		○	○	
Paspalum scrobiculatum		◎		○				○	○	
Echinochloa flumentacea		◎	△		○			○	○	
Brachiaria ramosa		◎		○	○			○	○	
Setaria pumila		◎		△				△	△	
Digitaria crusiata		◎		○						

◎, main ingradient used; ○, generally; △, rarely or suppliment mixed.

Cooking methods of boiled grains

Anna, a kind of boiled grain, is homologous to staple foods found the East Asian, such as, *bhat*, *chawal*, *sadam*, and *annamu* in India, and *meshi* in Japan. As illustrated in Figures 56-60, *anna* is prepared from crop grains either via the “draining off” or parboiling methods in India, while the “drying up” method is used in East Asia. The draining off technique, which is traditionally used in India, involves boiling grains in excess water and subsequently removing the hot water, resulting in soft grains that are non-sticky and flavor-full, qualities highly valued in Indian cuisine. The parboiled method is regarding as one of the oldest processing techniques for cereals, particularly for millet grains. “Parboiled” refers to pre-boiling raw grains before polishing them. This process polishes grains and enables nutrients from the seed coat to permeate the endosperm, thereby enhancing the nutritional quality of the polished grains. Recently, some urban populations in India have adopted the drying up method for rice preparation, making use of rice cookers to save time and retain nutritional value that might otherwise be lost via draining.

Anna is typically paired with various types of curry, *dal*, *sambar* (a kind of spicy stew), *rasam* (spicy soup), pickles, yogurt, salt, and plant oil, all of which are variations of rice *anna*, such as *pullao* and *biryani* (rich *pullao*), which are special festival foods in India.

Figure 56. Anna (boiled grain; *bhat*, *chawal* etc.) in India

a, Cooking utensils for the hot water removal method; b, anna made from rice; c, *chawal* made from foxtail millet and sorghum in farmer’s lunch box; d, *chawal* made from *samai* (*Panicum sumatrense*); e, *chawal* on the thali; f, *kesari bhat* made from rice and *upma* made from *Triticum durum*.

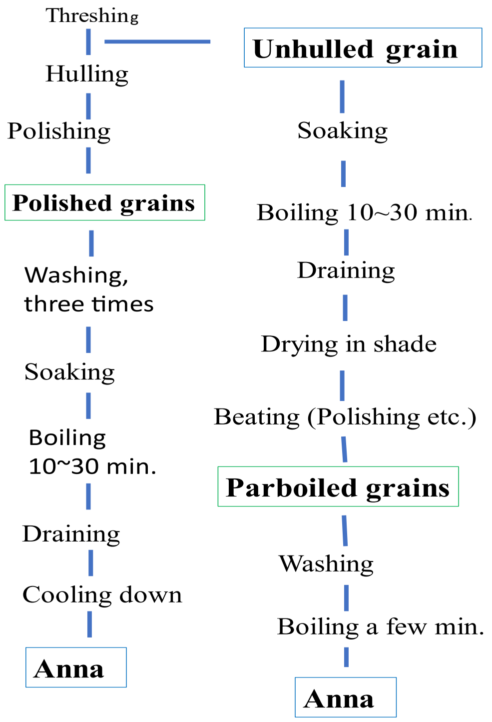

Figure 57. Cooking process of *Anna* (boiled grain) in South India

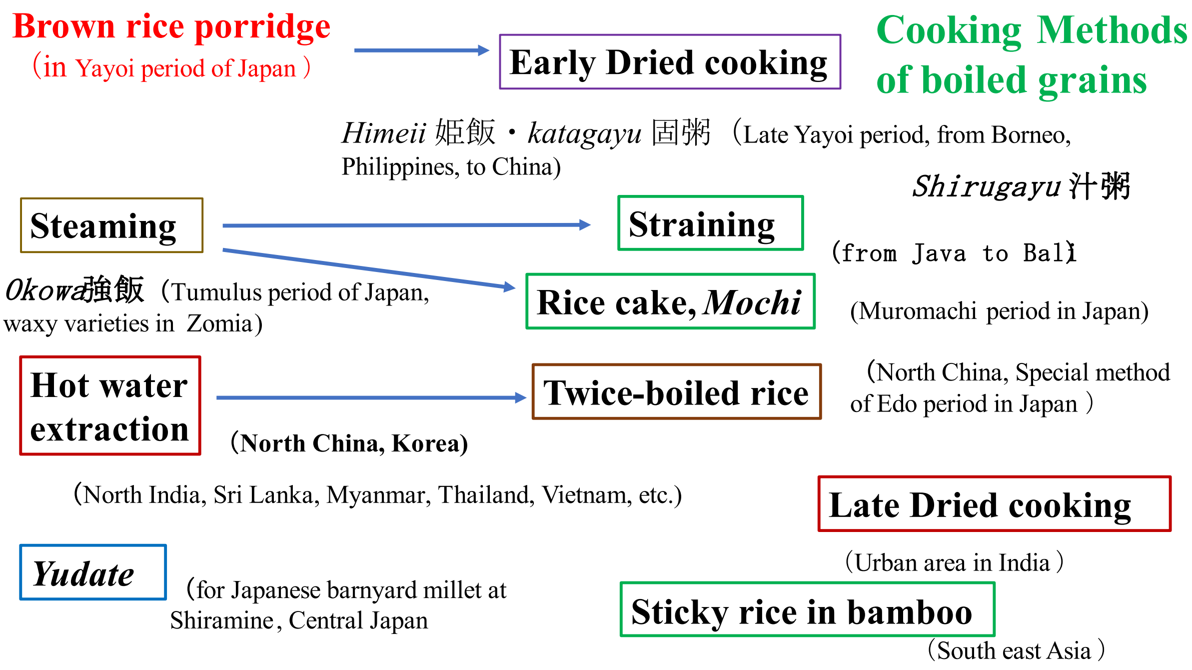

Figure 58. Cooking methods of boiled grains

Upma

Upma, made from ground coarse grains (Figures 59b and 60), is mostly breakfast food item. It is mixed with chili, ginger, ground nut, and yogurt or lemon juice.

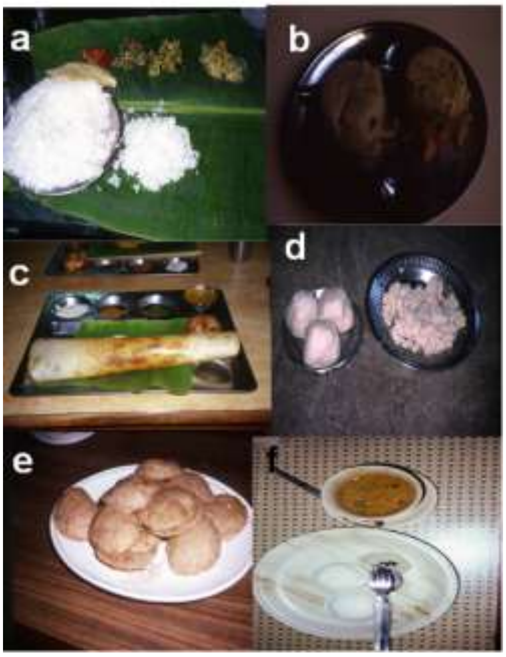

Figure 59. Cereal cookeries in the Indian subcontinent

a, A traditional boiled rice (*bhat*) with *papad*; b, *upma* and *khesari bhat*; c, *dosa*; d, *mude* and boiled grain made from *Brachiaria ramosa*; e, *puli*; f, *idli*.

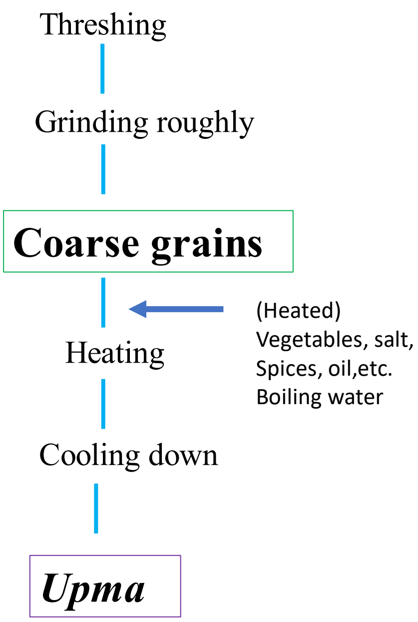

Figure 60. Cooking *upma*

Chapati, *roti*, and their variations

Chapati is a widely recognized type of Indian bread, frequently consumed throughout the country (Aziz 1983). It is an unleavened flatbread prepared from whole wheat flour (Figure 62). Commonly, it is wrapped in a dishcloth and kept warm in moderately heated ovens prior to serving with, typically, curry and dal stew (Figure 63a). The distinction between chapati and roti can be ambiguous; in certain regions of India, the term "*chapati*" is used, while "*roti*" elsewhere often denotes loaves purchased from shops or delivered from professional bakeries (Rangarao 1968). For clarity, pancakes prepared from whole wheat flour (*atta*) is referred to as *chapati* and the others from millet or bean flour as *roti*, in this text.

Parautha is another variation made from wholemeal flour, although it is much thicker than *chapati* and lightly fried in oil (*ghee*). *Puri* is a deep-fried *chapati* (Figure 61c) traditionally eaten with *chenna* chutney made with whole chickpeas at breakfast (Aziz 1983).

Nan is a semi-leavened bread made from fine wheat flour (*maida*) (Figures 61a and 64) and was introduced from West Asia in ancient times. Traditionally, *nan*, the perfect accompaniment to *tandoori* food, is usually prepared in clay ovens known as *tandoor* (Aziz 1983). Consequently, its preparation is uncommon among South Indian communities.

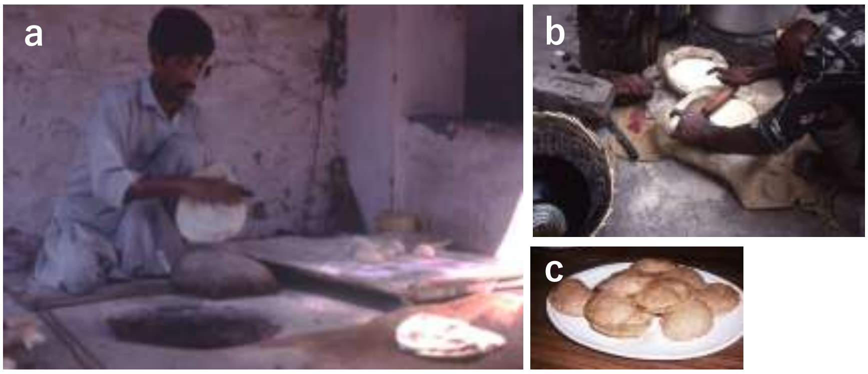

Figure 61. Food made from wheat, *Triticum aestivum*

a, *Nan*; b, *chapati*; c, *puri*.

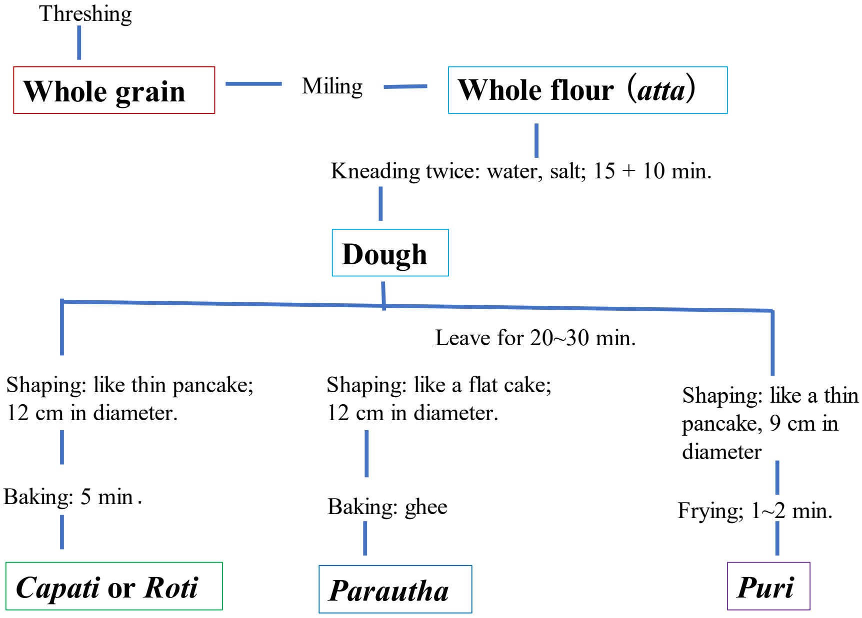

Figure 62. Cooking *chapati, parautha* and *puri*

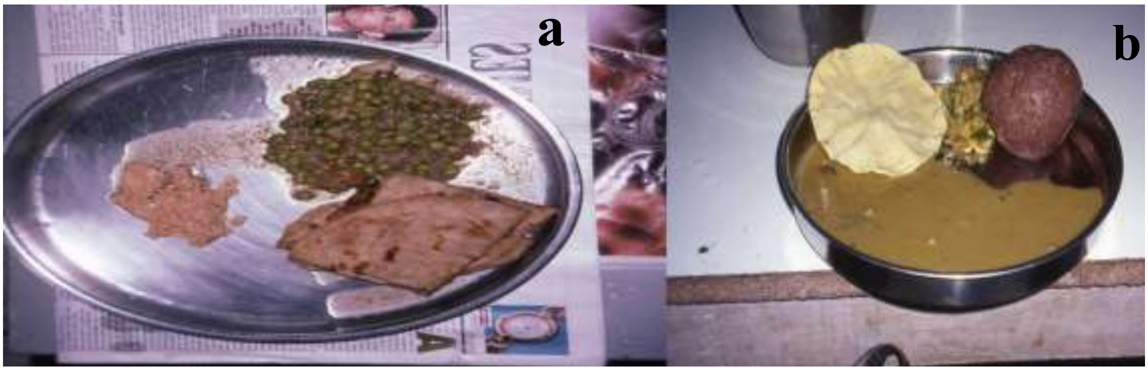

Figure 63. *Chapati* or *mude* on *Thali*

a, *Chapati* from wheat; b, *mude* from finger millet, *Eleusine coracana.*

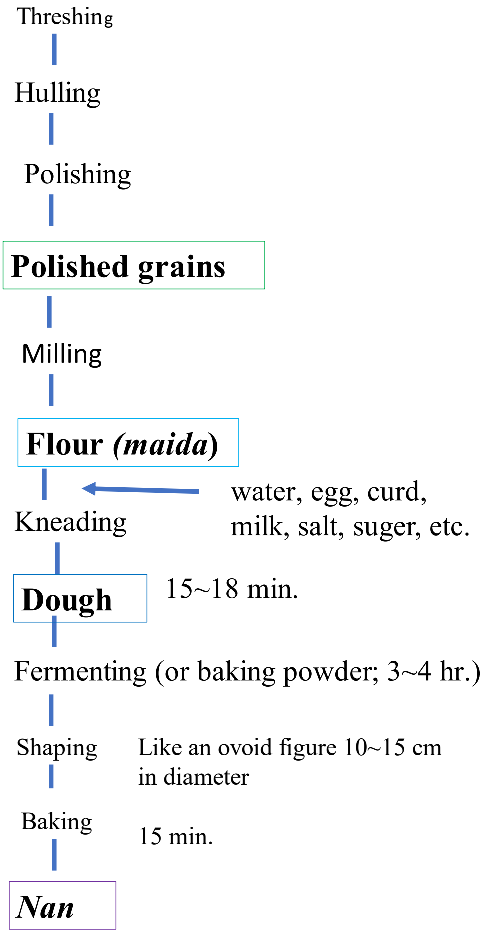

Figure 64. Cooking *nan*

Other fried foods

Vada (*amavadai*) is a disc-shaped or doughnut-like snack crafted from freshly ground *dal* or millet flour, spiced with chili, ginger, or onion, deep fried to golden brown color in peanut oil.

Papad is a crispy, salted wafer made with *dal* (many kinds of beans), vegetables, and cereals. It is a deep-fried circular wafer, thin as paper, with a golden yellow color (Figure 63b). These beans are *Cajanus cajan*, *Cicer arietinum*, *Lens culinaris*, *Pisum sativum*, *Vigna mungo*, and *Vigna radiata*.

Murukku is a coil-shaped rice (and *dal* or millet) flour snack molded by hand and fried in oil (Skelton and Rao 1975).

Dosa* and *idli

Dosa is a traditional South Indian leavened pancake prepared from a batter comprising ground parboiled rice (*cela*) and husked split black bean (*Phaseolus vulgaris* L.) (Figures 59c and 65). *Dosa,* which made also from wheat, oat, and pulse (Lal 1974), is stuffed with potato curry or dipped in *sambar* and chutney.

Idli is a leavened poundcake with the same ingredients as *dosa* (Figures 59f and 65), but is a steamed food, rather than fried, as *dosa*. *Idli* has been prevalent in South India for at least 40 decades, coinciding with increased rice consumption and the adoption of *idli katoris* (pressure cooker) became popular. Preparation of *dosa* and *idli* paste uses either manual or electromotive stone griding mortar. *Idli* is traditionally accompanied by *sambar* and chutney.

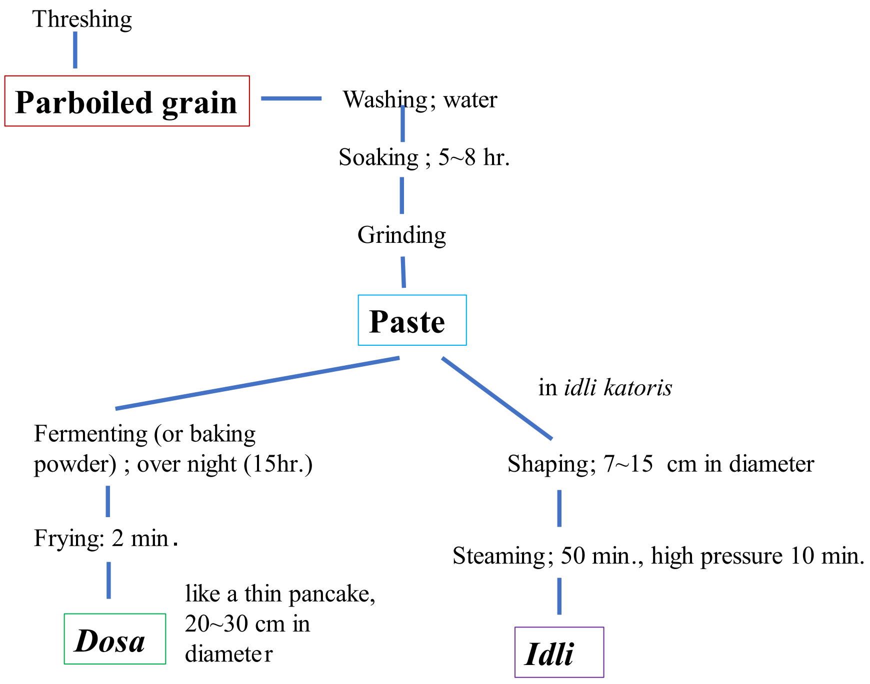

Figure 65. Cooking method of *dosa* and *idli*

Samosa is a deep-fried snack with a crisp, triangular wheat casing filled with spiced meat or vegetables. In AD 1300, Amir Khusrau described *somosa* as a dish of meat, *ghee*, onion among the Muslim aristocracy in Delhi (Figure 66a). Approximately 50 years later, Ibun Battuta called it *samusak*, describing it as "minced meat cooked with almonds, walnuts, pistachios, onions and spices placed inside an envelope of wheat and deep fried in *ghee*" (Achaya 1977).

Figure 66. *Samosa* and festival foods on banana leaf

Bread is prepared either unleavened (such as *chapati*, *puri*, *parautha*, *roti*) or leavened (like *nan* and other varieties), originating in the Near East, North Africa, India, and Europe alongside Triticeae grains. Noodles and *baozi* spread from China via Central Asia to Europe (Figures 67 and 68). There are three cooking methods of noodles: hand-pulled, stretched, of extruded.

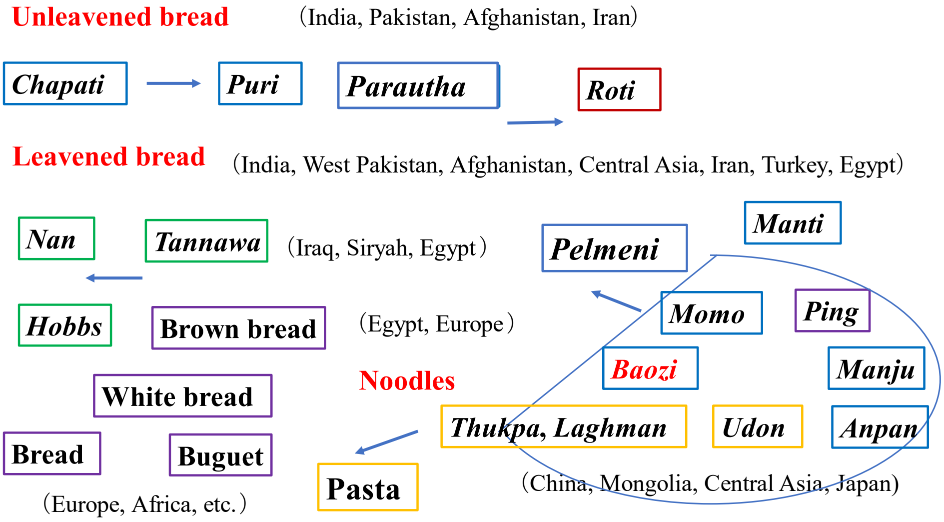

Figure 67. Cooking foods made from wheat flour

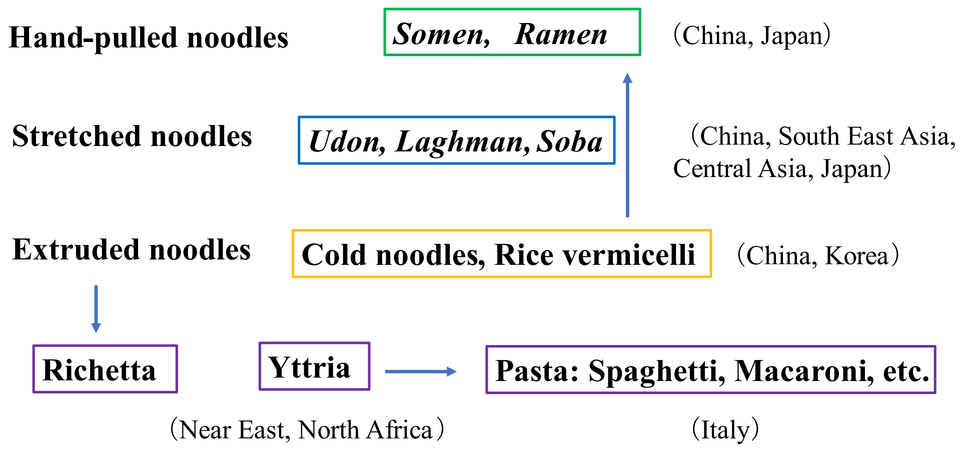

Figure 68. Three cooking methods of noodles

Mude* and *ganji

Mude (*kali*, *sankati*), a starch-paste prepared from millet flour, is analogous to *dhido* in Nepal and *oneri* in Japan. In South India *mude* and *anna* are the most common methods to prepare staple foods. *Ganji* is prepared from the same ingredients as *mude* (Figure 69, and requires a larger volume of water at boiling than *mude* (Figure 70).

Porridge is prepared from two millets in South Asia and Europe, and, based on the region, is referred to by various names, including *waji* (Halmahhera Islands), *mude* (India), *kochi* (Afghanistan), *mamalyga* (Caucasia), *ugre* (Turkey), *pcheno* (Bulgaria), *māmāliga* (Romania), *polenta* (Italy), and *millat* (France). In some countries, dumplings and flour porridge are prepared from these millets. Dumplings are also called *shito* (Ainu people in Hokkaido, Japan), *abai* (Formosa), sweet *ladu* (Pakistan). Flour porridge prepared from foxtail millet is called *kosayo* (Ainu people) and *ganji* (South India), among other names. Bread is primarily produced in India and Eastern Europe, and is called *roti* (India), *tathui* (North Pakistan), *kulsik* (Caucasia), and *prosenic* (Bulgaria).

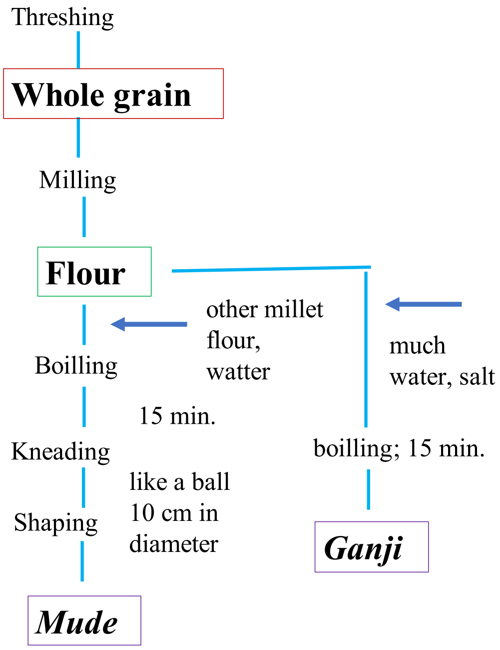

Figure 69. Cooking *mude* and *ganji*

Figure 70. Ganji made from Sorghum and finger millet

In Japan, sorghum is used to prepare various foods (Figure 71). For example, *dango* is made from finger millet in Gunma, *hecchoko-dango/ukiuki-dannngo* are made from sorghum in Iwate, and *mochi* from sorghum in Yamanashi. These millets and sorghum spread from Africa, via India and China to Far East Japan together with similar cooking methods. The agricultural exchange remains notable today.

Figure 71. Foods made from sorghum in Japan

a, *Dango* made from finger millet in Gunma; b, *Hecchoko-dango* made from sorghum in Iwate; c, *Ukiuki-dango* made from sorghum in Iwate; d, *Mochi* made from sorghum in Yamanashi.

Comparison of cultivation, processing, and cooking methods between *korne* and *korati*

The various food preparations derived from *korne*, *Brachiaria ramosa* are shown in Figures 40 and 59d. These can be classified into nine types, including as grain-based and flour-based foods. The grain-based foods include boiled grain (*anna*) and sweetened gruel (*kheer*).

The broken grain is used to prepare semi-solid porridge (*nuchina mudda*). Notably, parboiling is not customary for these grains. In the Tumkur district, farmers usually eat *anna* twice per month, reserving *kheer* for special occasions. Conversely, flour-based foods consist of unleavened bread (*roti*), leavened thin pancake (*dosai*), and a few deep-fried snacks (*nippattu*, *chakkulli*, *haralu*, *kodubale,* and *kadabu*). Grain-based foods are prepared by boiling with water, whereas flour-based by baking or frying with vegetable oil (Kimata, M., E.G. Ashok and A. Seetharam 2000).

Grain-based foods of *korne* are prepared as follows: 1) *Anna*. Polished grain is washed in water and boiled over high heat for approximately 6 min with occasional stirrings with a spatula; excess water is drained off; grain is steamed over low heat for 3 min. The cooked *anna* is served with *sambar*, a spicy vegetable stew, or yogurt. 2) *Kheer*. Grain is boiled with a larger quantity of water until tender, then, it is mixed with sugar or jaggery to achieve a gruel-like consistency. Fried groundnut is used for dressing the *kheer*. *Kheer* is a nutritious option for nursing mothers. 3) *Nuchina mudda*. The broken grains and finger millet flour are mixed in a 1:4 ratio and cooked in boiling water for 3 min, kneaded using a flat wooden stick, placed onto a wooden plat, kneaded again with an iron spatula, and hand-shaped into balls.

The preparation of the six flour foods are as follows: 1) *Roti*. The flour is mixed with water and kneaded, following which chopped onion is added to the mix, along with chopped green chilies, broken groundnut, and salt to taste. This thick dough is shaped into a flat round pancake by hand or rolling pin, and then cooked with a spoonful of oil in a frying pan (*hanch*) on both sides. 2) *Dosai*. Flour is mixed with water to form a thin batter, which is spread onto a frying pan and baked with a spoonful of vegetable oil for approximately 4 min. The baking process for *dosai* and *roti* are similar. *Dosai* is normally served with chutney (made of grated coconut and spices) and *sambar*. 3) *Nippattu*, *kodubale* and *chakulli*. Flour of *korne* is mixed with black gram flour or maida (specific fraction of wheat flour) in various proportions. Fried Bengal gram and groundnut are then mixed while preparing the dough for *nippattu*. 4) *Kadabu*. Flour of *korne* is prepared by mixing with water. A small quantity of the resulting dough is flattened using a rolling pin and stuffed with sweet ingredients, and then deep-fried in groundnut oil until golden brown.

In South India *korati*, *Setaria pumila* (syn. *S. glauca*), are used in various dishes, such as boiled grain (*anna*), unleavened bread (*roti*), porridge (*sankati*), and thin gruel (*ganji* or *peja*). *Korati* are often combined with little millet. Parboiled *korati* was reported only once during the survey in Orissa state. At Jalaripalli village, surveyed in 1997, six kinds of food were observed.

Preparation methods for *korati* grain foods comprise: 1) *Annamu*. The process is nearly identical to that of *anna* made from *korne* in Karnataka. 2) *Sankati*. Cooked *annamu* is kneaded by wooden sticks and shaped into balls. 3) *Ganji*. Cooked *annamu* is boiled with salt and pepper and thoroughly mixed. 4) *Uppitu*. The broken grains are rinsed, while vegetables, such as chili and onion, are sautéed in vegetable oil with coriander, mustard seed, chili powder, and salt before integrating with water and broken grains for boiling. 5) *Kheer*. Broken grains are boiled with large quantities of water until tender, excess water is drained, and grain is mixed with sugar.

Roti is the only flour food made from mixed ingredient, with similar process as the *roti* made from *korune*. Both *sankati* made from *korati*, and *nuchina mudda* made from *korne* are modified grain foods; however, the *mude* made from the other cereals are usually made from flour and thus generally classified as flour-based foods, which are relatively new variations.

History of processing and cooking methods for cereals

Ancient cereal processing predominantly involved simple porridge preparations. Coarsely ground porridge and roasted grains of barley/wheat are among the earliest documented foods (Figure 72). Also, roasted ground porridge is an ancient cooking method in Near East area. Figure 73 shows various methods for flour porridge preparations.

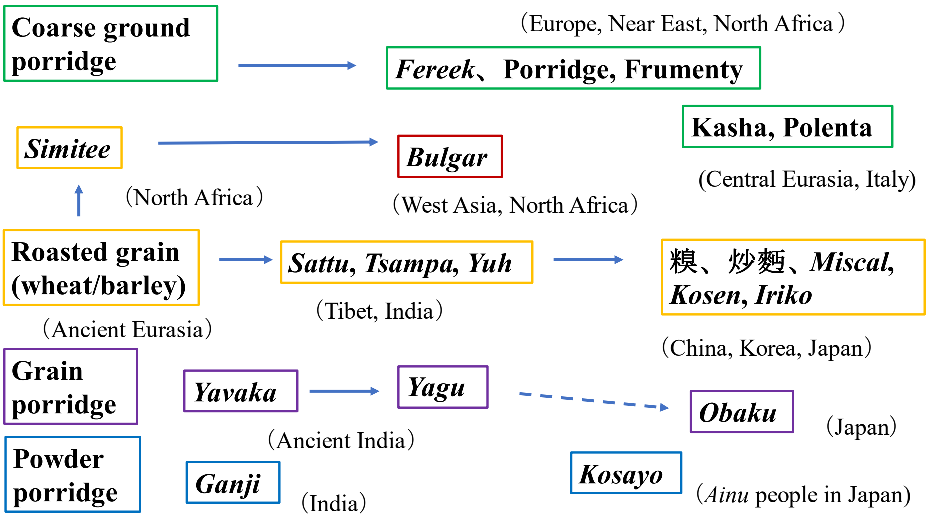

Figure 72. Types of porridge cooking methods

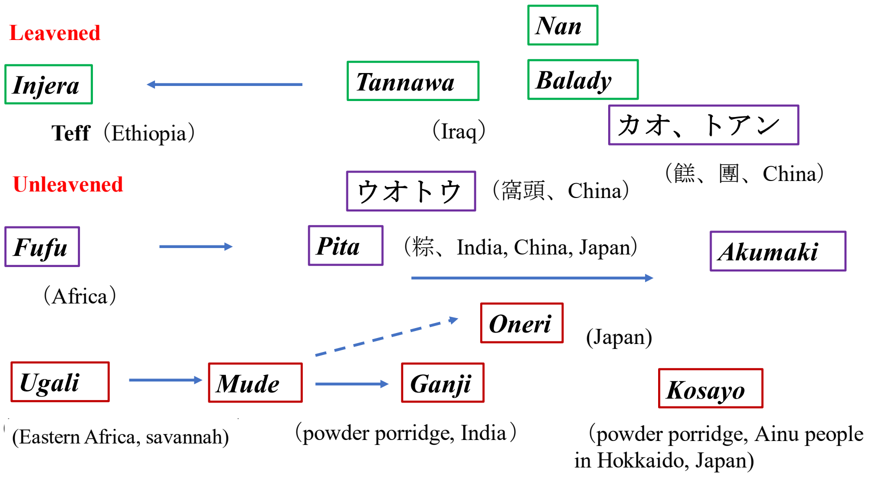

Figure 73. History of flour foods

Fermented drinks and foods

According to the Sherpa people, *kodo chan —made from finger millet*—has the best flavor among all grains, including rice, wheat, barley, and maize, in Nepal. While *Kodo* refers to finger millet in Nepal, it should not be confused with *kodora* (*Paspalum scrobiculatum*). Fermented *chan* (a crude alcoholic drink) or *roksi* (a distilled alcoholic drink) are the products of grain (Figures 74 and 75). The Newar people prepare *chan* using barely malt, whereas the Sherpas use malted buckwheat. Traditionally, Serpas drink diluted *kodo chan*, which is mixed with boiled water, through a bamboo straw (*chapshing*) from a vessel known as *tongba*.

Similarly, Non-alcoholic drinks are made in Caucasia and Eastern Europe, where they are called *buza* (Caucasia), *boza* (Bulgaria), and *mied* (Romania). Only in East Asia are alcoholic drinks made mostly from waxy grains. Prior to alcoholic fermentation, cereals, including several millets, are saccharized; in East Asia and India, this is done using *koji* (*Aspergillus oryzae*), while malting is used in Europe and Africa (Nakao 1967). This difference may be because the covered grains of Asian millets must be dehusked and polished before use, while the naked ones of African millets require no such processing.

Sorghum bicolor and *Pennisetum glaucum* are primarily used to prepare *roti*, while *Eleusine coracana* is mostly used for *mude* and the fermented alcoholic drink *chan* (Figures 74 and 75). *Hordeum vulgare* is used to produce a starter for fermented foods (Figure 75c, starter; 75d, a jar for fermentation; 75b, alcohol drink, *chan*, made from *Eleusine coracana*; 75e, yogurt, *dahi*.

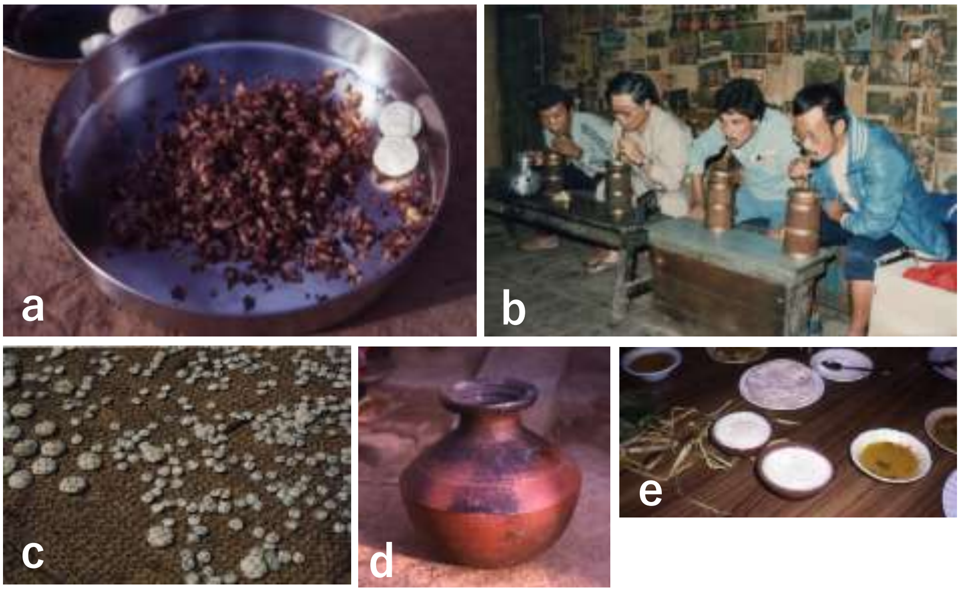

Figure74. Fermented foods

a, Yeast made from barley, *Hordeum vulgare*; b, vessel for fermentation; c, alcoholic drink, *chan* made from finger millet, *Eleusine coracana*; d, yogurt *dahi*.

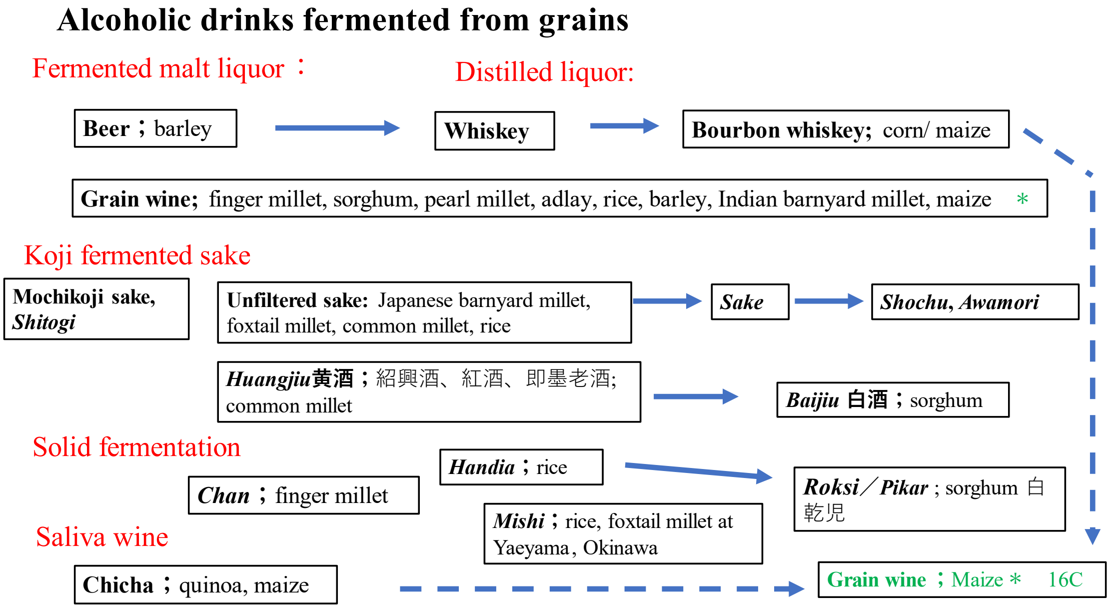

Figure 75. Alcoholic drinks fermented from grains

Food preparation and secondary compounds in grain

Eurasian culinary applications of common millet are classified into four processing methods: grain, coarse-ground flour, fine flour, and beverages. In Asian, non-glutinous varieties are primarily used for preparing boiled grain and porridge from the polished grains of non-glutinous varieties, whereas East Asian practices including steaming grains and *mochi* (a kind of cake) from the polished grains of glutinous varieties and ferment alcoholic drinks from the polished grains of non-glutinous and glutinous varieties. Inner Mongolians cuisine features daily consumption of milk tea with roasted grains. In Uzbekistan, colored grains are used to garnish *non* (a traditional bread), and milk porridge prepared from non-glutinous varieties is served for lunch at nursery schools. European traditions utilize coarse-ground flour for milk porridge, bread from fine flour, and polished only non-glutinous grains for non-alcoholic beverage fermentation. Classification based on the endosperm starch composition divides these grains into glutinous and non-glutinous types. The distribution of glutinous varieties of common millet and *Setaria italica* is predominantly limited to eastern Asia. Conversely, the geographical distribution of phenol color reaction to seed coats in *S. italica* closely parallels that of *Oryza sativa*, while the pattern in common millet diverges from those observed in *S. italica* and *O. sativa* (Sakamoto 1982, Kawase and Sakamoto 1982, Kimata and Negishi 2002).

Common millet local varieties are categorized by minor fatty acid composition, namely arachidic, behenic, and eicosapentaenoic acid. It is postulated that the ancestral AE type, which contains both arachidic and eicosapentaenoic acids, preceded the development of the AB type (arachidic and behenic acid) found across Europe and Asia, while the ABE (all three fatty acids) and O (no fatty acids) types might have originated in Central Asia and subsequently disseminated into Europe and Asia (Kimata et al. 2007).

Cereals with waxy endosperm are used as staple foods in Japan and other countries of East Asia. Waxy endosperm is found in common millet, foxtail millet, Job's tear (adlay), sorghum, rice, barley, and maize. Based on the data regarding these seven cereals with waxy endosperm varieties, the following conclusion can be drawn: The waxy varieties of foxtail millet (Figure 76), sorghum, adlay, rice, and maize are distributed over wide areas of East Asia, from the mountainous regions of Assam to Japan. The waxy forms of common millet and barley are confined to China, Korea and Japan, and are never found in the western half of Eurasia, areas ranging from India to Europe, Africa and the New World (Sakamoto 1982).

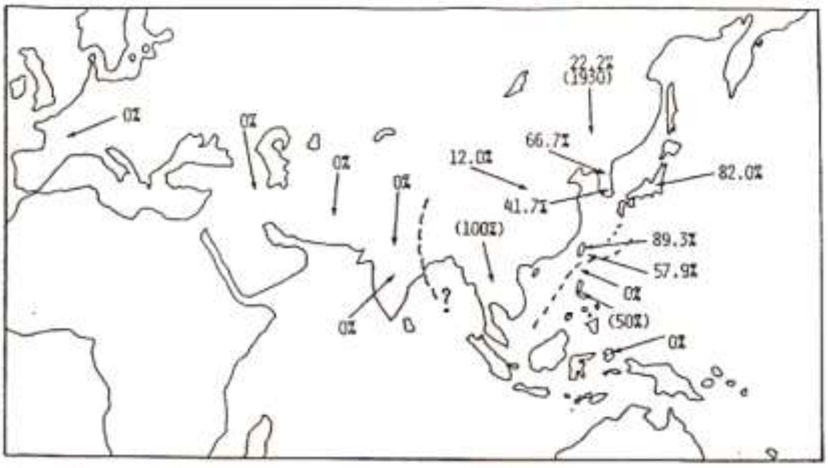

Figure 76. Geographical distribution of the waxy landraces of foxtail millet.
Each rate (%) shows the percentage of waxy landraces in respective region (Sakamoto 1982)

Eurasia millets are classified into four groups based on geographical origin, with each group spreading from its domestication region across Eurasia in prehistoric ages. Millets processing and cooking methods are central to the agricultural culture complex. Therefore, a comparative study on processing and cooking methods will help to clarify the geographical origin and dispersal of a given millet (Kimata 1987, 1989). Below, the processing and cooking methods used for the following four groups of millets are compared to study the relationship between processing and cooking methods and dispersal of millets into South and East Asia.

Common millet and foxtail millet (Group I)

Traditional foods and beverages from common millet and foxtail millet have been produced throughout Eurasia. In East Asia, boiled grain, gruel, *mochi,* and alcoholic beverages is popular; in Southeast Asia and Europe, meal porridge, bread, and non-alcoholic drinks are common (Table 43) (Sakamoto 1987a, partly modified). Boiled grain is made from waxy and non-waxy grain; the former grain is supplementally used for the latter and is referred to as *meshi* (Japan), *anna* (India), and *gharaji* (Pakistan) (Kawase and Sakamoto 1989). Gruel is made only from non-waxy grain in East Asia, while *mochi* is from waxy grain.

Table 43. Foods and drinks made from the grains of common millet and foxtail millet in Eurasia

Region	Types of cooking								
	Grain			Meal	Flour			Drink	
	Boiled grain	Gruel	Mochi	Porridge	Dumpling (dango)	Flour porridge	Bread	Non-alcoholic	Alcohlic
Japan									
non-waxy	○	○			△				
waxy	○		○		○	△		○	○
Korea									
non-waxy	○								
waxy	○		○						○
China									
non-waxy	○	○					○		○
waxy			○				○		○
Formosa									
non-waxy	○								
waxy	○		○		○				○
Batan Island				○					
Halmahera Islands				○					
India	○			○		○	○		
Pakistan	○				△		○		
Afghanistan				○			○		
Caucasia				○					○
Turkey				○					
Bulgaria				○			○		○
Romania				○					○
Italy				○					
France				○					

(Sakamoto 1987a modified)

Indian millets (Group IIa)

Indian cuisine has evolved over centuries, shaped by the diverse cultures introduced through successive invasions. Each wave of newcomers introduced new ingredients and culinary techniques, which were most prominently adopted and refined Northern India due to similarity in climate and landscape with their regions of origin. Furthermore, natural barriers and great distances hindered migration to the South (Sahni 1986).

Various cereals accompanied these cooking method as they spread across regions, particularly the Deccan Plateau. *Chawal* (boiled grain) prepared from Asian millets (Groups I and IIa) and rice is often made in Eastern India, while *roti* (bread) prepared from millets (mainly Group IV) and *Chapati* (unleavened bread) prepared from wheat modified from Mediterranean flour food frequently made in Western India (Table 44) (Kimata 1987).

Mude, modified from African meal porridge (mainly Group IV), is often prepared using various cereals native to South India and Nepal (also Japan), but not in North-Western and Central India. Indian culinary practices are largely categorized into two distinct regions: the North and the South, delineated by an axis running from Bombay (Mumbai) to Hyderabad. *Mude*, *ganji* (flour porridge), *dosa* (thin leavened pancake) and *idli* (leavened poundcake) are frequently consumed in South India. Tamil Nadu exhibits exceptional diversity in cooking styles, which gradually diminish toward the West, where staple foods, such as *chapati* and *roti*, predominate, especially among the farming community. In contrast, moving eastward shows similar trend, with farmers primarily consume *chawal*.

Table 44. Cereal cooking styles and ingredients in India

Grope	Cooking												Total
Ingredients	*Chawal*	*Upuma*	*Chapati*	*Roti*	*Non*	*Puri*	*Wada*	*Dosa*	*Idli*	*Mude*	*Ganji*	*Mavu*	
I													
Pan. miliaceum	○	△		○			△			○	○		6
Se. italica	○	△		△			○	○		○	○	○	8
II a													
B. ramosa	○		○	○						○			3
Ec. frumentacea	○	△					○			○	○		5
Pan sumatrense	○	○		△			○	○		○	○		7
Pas. scrobiculatum	○			○						○	○		4
Se. pumila	○			△						△	△		4
IV													
El. coracana	△	○		○			○	○	○	○	○		8
Pe. americanum	○	○		○						○	○		5
So. bicolor	○	○		○			○	○	○	○	○		8
O. sative	○	○					○	○	○	○	○	○	8
H. vulgare		○		○				○	○	○	○		6
T. aestivum			○		○	○		○		○	○		6
T. dicoccum		○							△				2
T. duram		△	△			○			△				4
Z. mays	△	○		○			△			△	○		6
Total	12	12	2	11	1	2	8	7	6	14	13	2	90

The grain of adlay **(Group IIb)** may be milled into flour, which is subsequently utilized in the preparation of bread or sweet dishes by frying the grain and adding sugar. The whole grain is also consumed raw as a snack, or fermented to produce beer in Assam (de Wet 1989). Adlay is used to make *prisan* (a non-alcoholic beverage) in Korea and Japan, meal porridge in Formosa and Halmahera Islands, and *mochi* in Korea and Formosa.

Japanese barnyard millet (**Group III)** serves as an ingredient in various Japanese foods, such as boiled grain (*meshi*), gruel (*kayu*), *hie-mochi* (made from non-waxy grains), meal porridge (*oneri*), dumplings (*dango*), flour porridge, and alcoholic beverages (*doburoku*). In Cheju Island, Korea, this millet is also used to prepare boiled grain.

African millets (Group IV)

Throughout Afro-Eurasia, people have used African millets to create various foods and beverages (Table 45) (Esele 1989; Jiaju 1989: Kimata 1983, 1987, 1989; Malleshi 1989; Rao *et al.* 1985; Sakamoto and Fukui 1972; Sakamoto *et al.* 1980; Shigeta 1987; Takei 1984). Boiled grain is mostly made from sorghum in South-East Asia, and is called, among others, *meshi* (Japan), *chawal*, *anna*, *bhat*, and *sadam* (Indian subcontinent). Boiled grain is traditionally made using the “drying up” method in East Asia and the “draining off,” hot water removal method in the Indian subcontinent. Gruel (grain) is not made from any African millet. *Mochi*, a kind of cake prepared from grains with waxy endosperm, is made from sorghum in Japan and Korea, where it is referred to as *mochi* and *docok*, respectively. Meal porridge is made from finger millet, sorghum, and pearl millet in East Asia, India, and Africa; it is called *oneri* (Japan), *dhido* (Nepal), *mude*, *kali*, *sankati*, *onda*, (India), *ugari* (Uganda), *kwon* (Sudan), and *tō* (Ghana). Meal porridge is a vital staple food in Africa and India. In Japan, dumpling (*dango*) is only made from finger millet and sorghum. Flour porridge is made from all three African millets, and is called *ganji*, *kulu* (India), *nyoka* (Sudan), and *koko* (Ghana). In the Indian subcontinent, bread (*roti*) is made from African millets only. Non-alcoholic beverages are made from only finger millet in India and Uganda, whereas alcoholic beverages are fermented from all three millets mostly in India and Africa; it is called *chan* and its distilled *roksi* (Nepal), *handia* (Bihar, India), *talla* and its distilled *araki* (Ethiopia), *kongo* (Sudan), *pito* (Ghana), etc.

Table 45. Foods and drinks made from the grains of finger millet, sorghum, and pearl millet in Afro-Eurasia

Crops/Region	Type of cooking								
	Grain			Meal	Flour			Drink	
	Boiled grain	Gruel	*Mochi*	Porridge	Dumpling (dango)	Flour Porridge	Bread	Non-alcoholic	Alcoholic
El. coracana									
Japan			△	○	○	△	○		
Nepal				○			○	○	○
India	△			○		○			○
Sudan				○					○
Ethiopia								○	○
Uganda				○		○			○
Burkina Faso				○					
So. bicolor									
Japan	△		○		○				
Korea	○		○						○
China									○
Halmahera	○								
India	○			○		○	○		
Sudan				○		○	△		○
Ethiopia									○
Burkina Faso				○					○
Pe. americanum									
India	○			○		○	○		
Sudan				○					△
Ghana				○		○			○
Burkina Faso				○					

Cooking method and foods made of millets

The domestication process of grain crops is well mastered in the Indian subcontinent, where several species of millet are domesticated. Cereals cooking is vital for agricultural culture complex, which encompasses vernacular terminology, religious significance, archaeological evidence, and other aspects (Maheshwari 1987, Sakamoto 1988).

Further analysis of these date will be presented in Chapter 7. My involvement in six expeditions dedicated to millet research has enable the collection of numerous accessions of millets and their relative species, along with information on their agricultural complex, sourced from hundreds of farmers across multiple villages and fields.

Ancient farmers in India domesticated six species of millet from wild relatives, facilitated by diffusion from humid paddy fields in Eastern India to dry upland rice fields in the Deccan Plateau in Southern India.

Indian food culture reflects the nation's heritage, historical development, religious beliefs, cultural practices, and geographical attributes (Sahni 1986). Staple foods prepared using grain crops are served with various spicy curries and legume *dal* stews (*dhal*). Each cereal is associated with unique regional cooking methods (Aziz 1983, Sahni 1986). Indian cuisine features distinct culinary techniques developed by each grain crop (Kimata et al. 2000). Comparative studies examining basic cereal cooking elements in India and Japan offer a scientific approach to clarifying the geographic origins and dispersal patterns of grain crops.

It is intriguing to examine the foundational elements of Indian cereal cooking and to identify similarities with Japanese methods for preparing grains. Conducting a comparative of these cooking methodologies offers a scientific approach that can help clarify the geographical origins and the spread of specific grain crops.

Across different cultures, numerous food varieties are prepared using millets and cereals. In particular, dishes such as *bhat* (*meshi* in Japanese), *roti* (*pan*), and *mude* (*oneri*) are commonly prepared, as they frequently utilize most of the cereals listed in Table 46 (Kimata 1987). *Bhat* is the most popular food among these, characterized as a boiled grain dish made with all the essential ingredients shown in Figures 77 and 78. The origins of *bhat* trace back to ancient China, after which it was introduced to the Indian subcontinent through Eastern India. Another staple, *roti,* is a popular food made from cereal flour. Its origin can be traced to the preparation of wheat bread in the Fertile Crescent. Over time, this culinary tradition was brought to the Indian subcontinent via Western India, where it became an integral part of local diets.

Mude, also known as *oneri*, is another popular food prepared form cereal flour. Its method of preparation and culinary lineage can be linked to the cooking of *ugari,* a dish that originated in Eastern Africa and was introduced to the Indian subcontinent through the Arabian Peninsula.

Sorghum bicolor and *Pennisetum glaucum* are mainly used for making *roti*, while *Eleusine coracana* is mostly used for making *mude* and fermented alcoholic beverage *chan*. Other millet species are mainly used for *bhat*. *Mavu* is special food made from the raw flour of *Setaria italica* and *Oriza sativa* as offering for gods and goddesses during festivals. Nine foods are made using *Brachiaria ramosa*, *mude* is made using *Eleusine coracana*, and *chapati* is made using wheat, *Triticum aestivum*. With respect to fermented foods, a starrer is made from *Hordeum vulgare*.

Details of these culinary practices are presented in Tables 46 and 47. *Upma* is a coarse-grain food. *Dosa* is a thin leavened pancake, and *masala dosa* is stuffed with potato curry. *Idli* is a leavened pound cake made using the same ingredients as *dosa*. *Vada* is a cake made from freshly dal or millet flour. *Ganji* is a very thin starch-paste made from the same ingredients as *mude*.

Table 46. Millets and associated foods in the Indian subcontinent

Species name	Food									
	Indian name	bhat	upuma	roti	vada	dosa	idoli	mudde	ganji	mave
	Japanese name	meshi		pan	age pan		mushipan	oneri	konagayu	shitogi
Sorghum bicolor		○	○	◎	○	△	○	○	○	
Pennisetum americanum		○	○	◎				○	○	
Eleusine coracana		△	○	○	○	○	○	◎	○	
Setaria italica		◎	△	△	○	○		○	○	○
Panicum miliaceum		◎	△	○	△			○	○	
Panicum sumatrense		◎	○	△	○	○		○	○	
Paspalum scrobiculatum		◎		○				○	○	
Echinochloa flumentacea		◎	△		○			○	○	
Brachiaria ramosa		◎		○	○			○	○	
Setaria pumila		◎		△				△	△	
Digitaria crusiata		◎		○						

◎, main ingradient used; ○, generally; △, rarely or suppliment mixed.

Number of ingredients for South-East Indian cooking styles

Table 47 lists the number of ingredients used in 12 main foods. *Chawal* (*bhat*,48) and *roti* (42) use the most ingredients, followed by *ganji* (36) in Tamil Nadu and Mahdia Pradesh. M*ude* (*mudde*, 27) is cooked using many ingredients in South India, and *upma* (26) in Karnataka and Tamil Nadu. *Chapati*, *nan*, and *puri* made from wheat flour are common in West India. *Vada* is common primarily in Tamil Nadu, *dosa* is in South India, and *idli* is in Karnataka. *Mavu* is unique to Tamil Nadu. The number of ingredients—and thus diversity—decreases moving north from Tamil Nadu, especially for millet dishes.

Table 47. Number of ingredients for South-East Indian cooking styles

Cooking style	Number of ingredients							Total
	Maharashtra	Mdhya Pradesh	Karnataka	Tamil Nadu	Andhra Pradesh	Orissa	Bihar	
Chawal	3	8	6	9	8	7	7	48
upma	0	0	9	11	2	3	1	26
chapati	1	1	1	2	1	1	1	8
roti	4	10	7	4	6	2	9	42
nan	1	0	1	0	0	0	0	2
puri	1	0	1	1	1	1	0	5
vada	1	0	1	8	0	0	0	10
dosa	0	0	4	7	5	1	1	18
idli	1	0	4	1	1	1	1	9
mude	0	0	7	12	7	1	0	27
ganji	2	10	3	11	5	5	0	36
mavu	0	0	0	2	0	0	0	2
Total	14	29	44	68	36	22	20	233

Table 48 lists the cereals and their ingredient counts used in cooking in the Deccan Plateau. Among the primary 12 cereal-based dishes, rice (34) is used most frequently, followed by *samai* (25), foxtail millet (25), and *ragi* (finger millet, 23). Other cereals are used for cooking foods throughout the Indian subcontinent. However, barley, emma, and durum wheat are cultivated only in mountainous villages. *Korati* (8) and *korne* (4) are cultivated only at the confined area in Eastern Decan. The methods of processing/cooking are summarized in Figures 77 and 78.

Table 48. Number of ingredients in cereals cooked in the Deccan Plateau

Ingredients	**Number of ingredients**							**Total**
	Maharashtra	**Mdhya Pradesh**	**Karnataka**	**Tamil Nadu**	**Andhra Pradesh**	**Orissa**	**Bihar**	
El. coracana	1	1	6	7	4	3	1	23
Pe. americanum	1	1	2	4	2	1	2	13
So. bicolor	0	2	4	7	3	0	1	17
H. vulgare	0	2	0	5	0	0	0	7
T. aestivum	3	3	3	4	2	2	1	18
T. dicocum	0	0	0	1	0	0	0	1
T. durum	0	0	2	3	3	0	0	8
P. miliaceum	0	0	4	5	1	0	2	12
S. italica	1	2	5	7	5	3	2	25
O. sativa	5	3	6	7	5	4	4	34
B. ramosa	0	0	3	0	0	1	0	4
Ech. frumentacea	0	3	0	5	2	2	1	13
P. sumatrense	3	3	5	6	4	2	2	25
Pas. scrobiculatum	0	3	2	3	1	2	2	13
S. pumila	0	3	0	0	4	1	0	8
Z. mays	0	3	2	4	0	1	2	12
Total	14	29	44	68	36	22	20	233

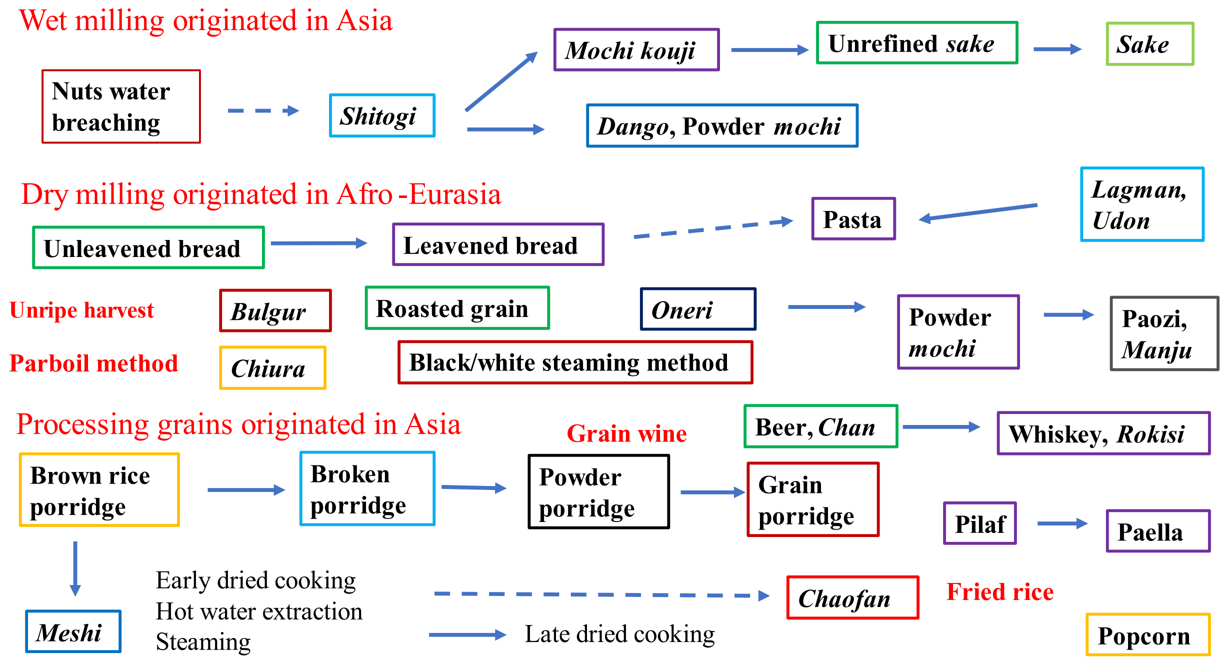

Figure 77. Milling, processing, and cooking cereal grains

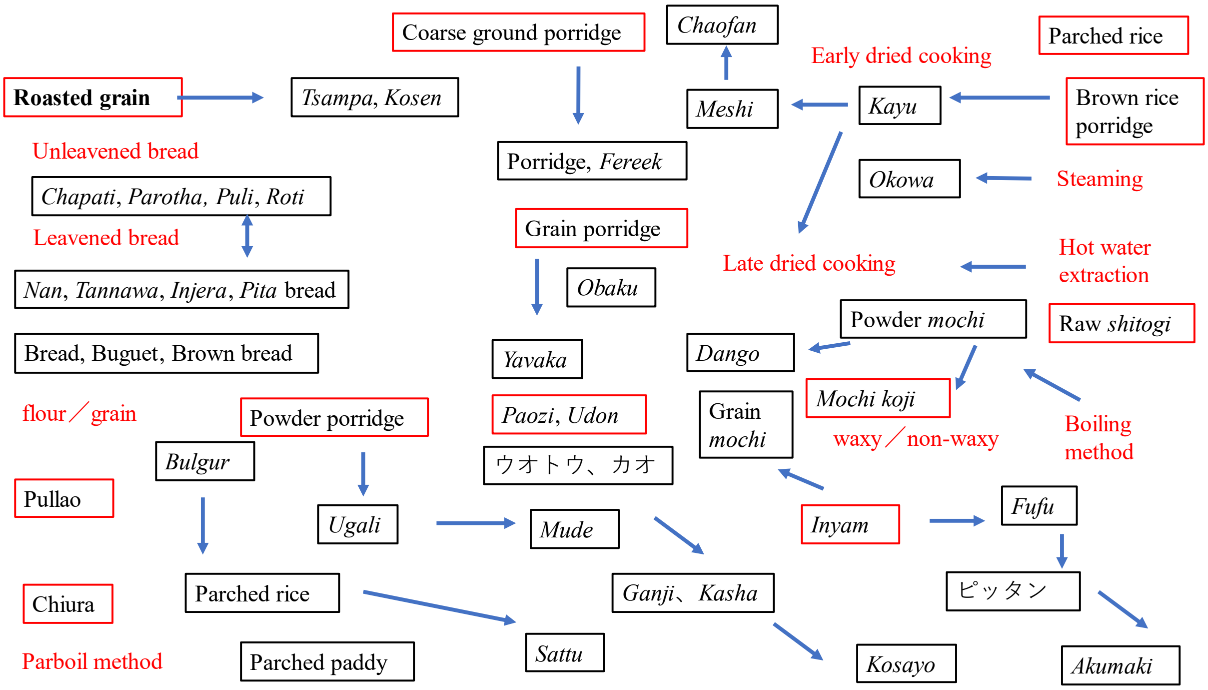

Figure 78. Historical relationships among processing and cooking grains

Processing cereal seed grains for cooking is challenging; however, these grains can be stored long term, making them suitable stable foods. Many types of cereals were introduced to the Decan Plateau through various cooking techniques from different regions. The rich biocultural diversity of cereals, especially of millets, has ensured daily security, as these grains became deeply integrated within the Indian subcontinent.

In Eastern India, *Chawal* (syn. *bhat*, boiled grain) is prepared using Asian millets and rice. By contrast, in Western India, *roti* (bread) are prepared from millets and *chapati* (unleavened bread) from wheat modified from Mediterranean flour food (Kimata 1987).

The integrating hypothesis for the dispersal route of Indian millets is illustrated in Figure 79. *Echinochloa furumentacea*, *Panicum sumatrense,* and *Paspalum scurobiculatum* were secondary crops to upland rice. Initially, their ancestor plants were companion weed from related species that invaded paddy fields in humid regions of Eastern India. These weeds eventually became backup crops in upland rice fields and later spread to the drier Deccan Plateau (Kobayashi 1987, 1989). *Brachiaria ramose* and *Setaria pumila* were referred to as tertiary crops to the other millet species domesticated from their relative weeds in upland fields. *Digitaria cruciata* is a more recent crop developed from the relative weed growing in maize or vegetable plots in Kashi Hill, Meghalaya, and is restricted to the same area (Singh and Arora 1972).

Indian millet species were domesticated as agricultural practices moved from humid paddy fields in Eastern India to drier upland rice fields in the Deccan Plateau, Southern India. Rice was first domesticated near the Pearl River, and spread from South China, via Zomia, into East India.

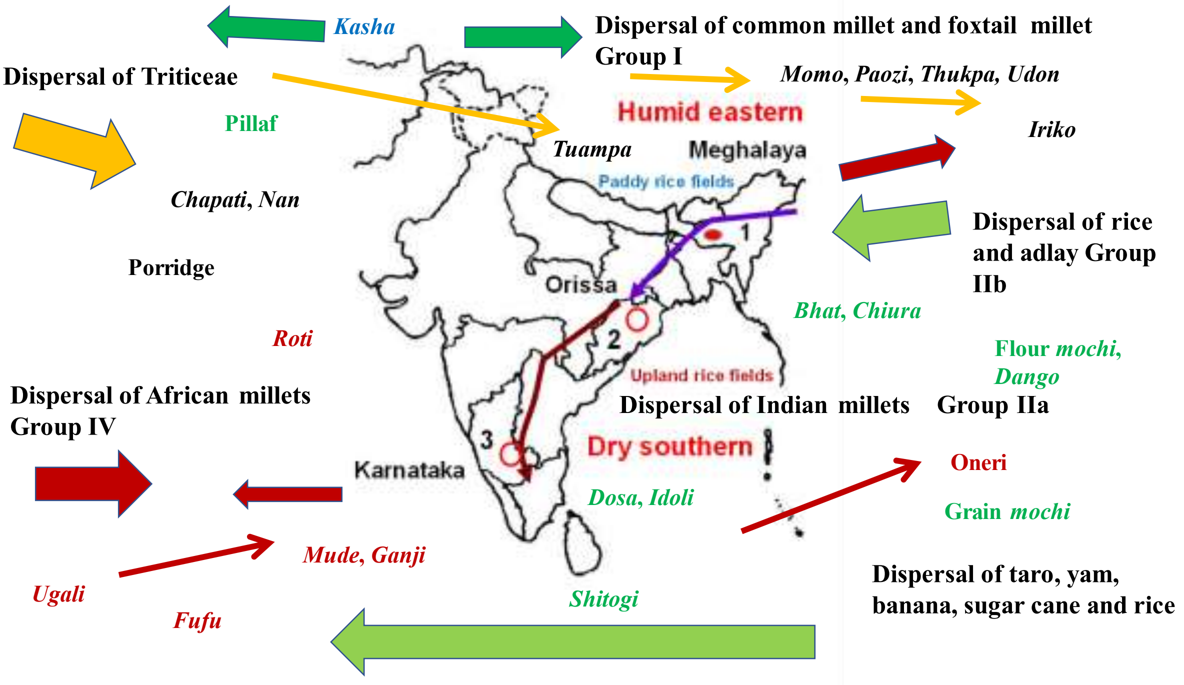

Figure 79. Dispersal of crops across the Indian subcontinent

Up-to-date utilization of millet in Japan

In Japan, six types of millet have traditionally been cultivated: common millet, foxtail millet, adlay, Japanese barnyard millet, finger millet, and sorghum. Japanese cooking evolved under the influence of Africa, India, and Chinese agricultural complexes. Tracing the origins of millet dishes reveals connections with cooking methods from other regions; for example, India's *mude* is made primarily from African millets and parallels Africa's *ugari*. Similar foods exist in in Nepal as *dhido* and as *oneri* in Japan. The *ugari*-style cooking, using various millets, maize, and buckwheat (*Fagopyrum esculentum* Moench.), illustrates a shared culinary heritage that reached the Far East.

Today, Japan's staple foods are primarily boiled grain prepared from rice or bread from wheat flour. The above-mentioned six millets are rarely cultivated, except in a few mountain villages. Recently, however, Asian millets, common millet, foxtail millet, and Japanese barnyard millet have been used to prepare efficacious foods against atopic dermatitis, an allergic disease, for Japanese children highly sensitive to other staple foods, such as rice and wheat. Millets are being experimented with in products like breads, cookies, and noodles. Millet derived foods are also efficacious for arterial sclerosis, colon cancer, and anemia, since millet has more dietary fibers and iron ions than rice. Dietary fibers reduce blood cholesterol levels and sustain good conditions for bacterial flora in the colon. Iron ions promote erythropoiesis.

Millets remain valuable crops in semi-arid and mountainous regions, and should be preserved alongside in traditional cooking practices, religious festivals, as important materials for future utilization.

Millet is expected to gain a more significant role as a food grain and fodder in the near future due to desertification and rising population, while chiefly used for food, millets may sever other purposes. Their leaves and stems are nutritious cattle fodder, their cultivation supports sustainable agriculture together with the livestock farming. The small grains of millets can be used to feed pet birds, a major market in European countries and Japan.

It is essential to maintain traditional millet-based foods while also developing modern millet products. To maximize millet's utility, comprehensive strategies involving interdisciplinary research, industry, and international cooperation are necessary.

Chapter 7: A New Model of Millet Dispersal Hypothesis

An influential hypothesis regarding the origins of domesticated plants and the development of agricultural complexes had guided research into the domestication of millets (Nakao 1966, 1972; Sakamoto 1988, Sasaki 1994). As discussed in this chapter, this hypothesis warrants refinement to reflect current understanding. A pivotal development in this field is the clarification of the domesticated origin of rice, which has shifted from Bihar, Eastern India to the Pearl River region of Southern China (Huang, Kurata et al. 2012). The oldest rice grains had been discovered at Shangshan, Pujiang, China, indicating that rice domestication began around 11,000 BP (Xinhua News 2020).

Nakao's hypothesis

Nakao's hypothesis can be summarized in eight key points:

1) Features of the Root Cultivation Farming Cultural Complex

- Farming without seeds
- Progress in using polyploidy species
- Lack of beans and oil crops
- Spot sowing performed using digging sticks
- Evolved from back garden cultivation to swidden (slash-and-burn) agriculture
- Job's tear important crop in this complex
- Root Cultivation Farming system dispersed to Africa

2) Finger millet was an essential element of the cultural complex on Savanna Farming. Common millet and foxtail millet were domesticated in the dry regions from Northwest India to West Pakistan. *Korati* (*Setaria glauca*, syn. *S. pumila*) in Bombay State (now Maharashtra and Gujarat), originated in the Indian subcontinent. Additionally the genus *Echinochloa* was domesticated as *E. frumentacea* in the Indian subcontinent and as other species in the temperate zones of evergreen broadleaf forest, eventually spreading to Japan.

3) The characteristics of domesticated species were fundamentally different from those of weeds, and the relationship between them was fully competitive. In the Savanna farming complex, secondary crops were not domesticated, primarily due to the farming practices employed. Farmers practiced drilling millet seeds and performed careful weeding, which prevented the domestication of these secondary crops. In contrast, among the tribe Triticeae, weedy species were not considered adversaries, and many secondary crops were domesticated from their related weed species.

4) The Savanna farming complex began with the gathering of wild grains for foods during monsoon season. In areas receiving heavy rainfall, large populations of Poaceae plants thrived in wetlands. Human selection focused on a wild rice, a type of millet, which was subsequently domesticated to grow in new habitats, such as paddy fields. Rice was not regarded as a special crop among millets and, thus, a distinct rice cultural complex did not develop. Instead, rice cultivation was included within the broader savanna farming complex, which itself had been influenced by the root farming

complex.

5) Rice cultivation began as a type of millet farming in the Indian subcontinent. It was initially grown in paddy fields located on plains. Following its spread eastward, new varieties of upland rice emerged in the mountainous regions of East Assam, where environmental conditions facilitated their differentiation.

6) The practice of transplanting rice closely mirrored that of finger millet. Finger millet establishes itself well even in upland fields when transplanted in July, during the monsoon rains. Rice transplanting may have been modeled after finger millet cultivation practices. This technique may have originated in Bihar within the Indian subcontinent.

7) The mountainous areas of Assam were characterized by the Root Farming Complex, where farmers cultivated root crops using digging sticks. Upon the dispersal of rice to this region, farmers adopted similar methods, sowing upland rice on swidden fields using hill seeding techniques common to root crops. Upland rice was cultivated alongside millet varieties such as foxtail millet and common millet, as well as the waxy variety of Job's tear. These grain crops shared the trait of being annual plants.

8) When farmers harvested immature seed grains, the high water content made them unsuitable for storage. To address, this, the grains were consumed or processed immediately. One method involved making *yakigome* (parched rice): farmers harvested early rice grains (waxy), steamed them in a pot, pounded them in a mortar to remove the husks, and produced flatten rice. This pregelatinized starch rice possessed excellent storage properties, and could be eaten simply by adding water. Japanese barnyard millet was a staple food until the Meiji period in Japan. The refining methods, known as "*shiromushi*" and "*kuromushi*," involved seaming and then polished the grains.

Reconsideration on the origins of main foods based on their history and archaeology

The first occurrence of grain crops in South Asia is detailed in Table 50, adapted from Fuller et al. (2001) with additional information (Fuller and Madella 2001; Fuller, personal communication).

Early Phase (around 4500 BC): At Harappan sites, *H. vulgare*, numerous *Triticum* species, and a few *Avena sativa* were detected.

Mature Phase (around 2600 BC): *O. sativa* (in large amounts) and *Panicum miliaceum* (in small quantities) were present.

Late Phase (around 2000 BC): Numerous *Setaria* species and *Sorghum bicolor,* and trace amounts of *Pennisetum glaucum* (syn. a*mericanum*) were found.

Early South Indian Sites (2300–1800 BC): Abundant *Brachiaria ramosa* and *Setaria verticillata* as well as trace amounts of *Panicum sumatrense* and *Setaria pumila*.

Late Sites (1800–1200 BC): Traces of *Paspalum scrobiculatum* and abundant *Echinochloa* cf *colona* (possibly *Echinochloa frumentacea*).

The chronological sequence of Asian millet occurrences is as follows: *Panicum miliaceum*, then *Setaria* species, followed by *Brachiaria ramosa*, *Setaria verticillata*, *Panicum sumatrense*, and *Setaria pumila*, and finally *Echinochloa* cf *colona* and *Paspalum scrobiculatum*. However, *Brachiaria ramosa*, *Setaria verticillata*, *Setaria pumila*, and *Echinochloa* cf *colona* were likely initially gathered as wild grains.

Table 50. Summary on the first occurrence of grain crops in South Asia

Species	Early	Mature	Late		(South India)			
Period	4500 B.C.-	-2600 B.C.	-2000 B.C.	2300-1800 B.C.	1800-1200 B.C.	-0 A.D.	1500 A.D.	1900 A.D.
Paspalum scrobiculatum					trace			
Panicum sumatrense				trace	a few			
Echinochloa cf. colona					many			
Brachiaria ramosa			wild?	many	many			
Setaria verticillata			wild?	many	many			
Setaria pumila			wild?	trace	trace			
Setaria sp.			a great many					
Digitaria cruciata								domesticated
Digitaria sanguinalis							(unknown, disapeared)	
Panicum miliaceum		a few						
Panicum sp.			a few					
Setaria italica			possible					
Eleusine coracana			?	possible				
Sorghum bicolor			many					
Pennisetum glaucum			trace	trace	trace			
Coix lacryma-jobi						possible		
Oriza sativa		many		trace	trace			
Hordeum vulgare	a great many			many	many			
Triticum dicoccum				trace	trace			
Triticum durum/aestivum				many	trace			
Triticum sp.	a great many			many	many			
Avena sativa	a few							
Zea mays							introduced	

Modified and Based on Fuller et al. 2001, Fuller and Madella 2001, and Fuller (personal communication).

The vernacular names of cereals used in Indian cooking reflect the diversity of regional practices and linguistic traditions (Tables 31 andd 32). Various millets have been cultivated and incorporated into a wide range of dishes, particularly in South India. Each type of cookery is often associated with specific local terminology, though there are some exceptions involving millets and rice.

Boiled grains are commonly referred to as *chawal* or *bhat* across India. However, regional variations exist: in Andhra Pradesh, they are called *annam;* in Tamil Nadu, as *sadam* and *soru*; and in Karnataka, as *anna*. Thick porridge also carries different names depending on the area—*onda* in Orisa, *samkati* in Andhra Pradesh, *kali* in Tamil Nadu, *mude* and similar terms in Karnataka, and *dhido* or *senne* (Sherpa) in Nepal. Thin porridge is called *bari* in Uttar Pradesh, *peja* in Madhya Pradesh, *ambil* in Maharashtra, *jau* in Orissa, *ganji* in Andhra Pradesh and Karnataka, and *kulu* in Tamil Nadu. Additionally, in Tamil Nadu, *mave* is a raw flour food offered to Hindu gods, prepared exclusively from foxtail millet and rice.

Farmers have developed an acute awareness of the status of millets and their relative weeds throughout the domestication process. This symbiotic relationship has been reconstructed using field observations, botanical experiments, archaeological evidence, and linguistic studies. The Eastern Ghats and Southern Deccan Plateau are regions where Indian millets and their relatives have historically been widely cultivated with their relative species, with vernacular names reflecting this agricultural heritage.

Linguistic analysis reveals connections between Old Indo-Aryan and Dravidian languages are the vernacular names of millets. Notably, *Brachiaria ramosa* and *Setaria pumila* originated as weeds around upland rice fields and evolved through mimicry and companionship with *Panicum sumatrense* and other grain crops. *Brachiaria ramosa* has since become an independent crop cultivated in pure stands, while *S. pumila* is often grown as a mixed crop with *Panicum sumatrense* and other millets.

Brachiaria ramosa and *Setaria pumila* are considered “tertiary crops,” functioning as double secondary crops for other millets and upland rice. Archaeological evidence supports this evolutionary sequence of millet occurrence at historical sites. The domestication center for millets encompasses the Eastern Ghats and Southern Deccan Plateau.

The history of food preferences and ingredient changes is summarized in Table 51. Humans have been notably conservative in their food preferences, with ingredients slowly evolving. During the Paleolithic age, barley porridge was the staple, shifting to wheat during the Neolithic age. Bread made from 100% wheat was considered a luxury food, reserved for high-ranking individuals, while ordinary people consumed millet-based foods, oat porridge, and rye bread (*maslin*).

Social discrimination was evident in food access: farmers cultivated wheat and rice but primarily ate oat and millets until the Middle Ages. The introduction of maize and potatoes from the New World was initially met with resistance in Europe; maize was accepted only in the 16th century, while potatoes were fed to pigs and maize to cows until the 19th century. It was only after the development of the Agri-pastoral complex. After that European people had become to eat much volume of meat. Because the Agri–pastoral Complex that Europeans began consuming larger quantities of meat, leading to a significant increase in both human and domesticated animal populations.

Crop evolution has progressed from the subsistence farming for survival, to grain taxes paid to rulers until the Middle Ages, and finally to commercial merchandise for urban populations in modern times. Throughout human history, grain crops—especially millets—have faced discrimination and prejudice. Millets have often been labeled as “Orphan crops,” neglected and underutilized species (Pdulosi et al. 2022). This status was recognized by the United Nations General Assembly, which declared 2023 the International Year of Millets during its 75th session in March 2021. I delivered a short speech, “A historical sketch of millets in Japan” at a related webinar.

Table 51. Historical discrimination and prejudice on foods (cereals/beans/tubers)

Region/People	Main food	Wheat	Rice	Maize	Millets	beans	Tubers
Europe	wheat	grain spilit		not food for European			not food for European
Ruler	tax	bread wheat		New ruler had eaten bread wheat, subjuugated people had eaten emmer/spelt wheat			
City people	not cultivate	bread wheat					
Farmer	cultivate	barley, rye, oat			foxtail/common millet	pea, lentil, faba, chick pea	potato for pig
Livestock	feeding	increase in meat - eating	culms,leves, weed, wild	feeding for cattle			
Wild animal	predation	wild animals and plants					
Africa	sorghum, pearl millet						
Ruler	tax	Wheat					
City people	not cultivate	Wheat					
Farmer	cultivate		wild grains		finger/pearl millet, tef, sorghum,	cawpea	Yam
Livestock	feeding		culms,leves, weed, wild				
Wild animal	predation	wild animals and plants					
Asia	rice, taro						
Ruler	tax		rice				
City people	not cultivate		rice				
Farmer	cultivate	wheat, barley	rice		foxtail/common millet, finger millet, backwheat	soy, azuki	taro, Yam, potato, sweet poteto
Livestock	feeding		culms,leves, weed, wild		grains for human, stems/leaves for cattle	culm and weed, wild	
Wild animal	predation	wild animals and plants					
Meso/South America		maize, potato					
Ruler	tax		maize				
City people	not cultivate		maize				
Farmer	cultivate		maize	saui, mango, quinoa, amaranth	kidney beans, groundnut		
Livestock	feeding						
Wild animal	predation	wild animals and plants					
Japan			*mochi* new year, *inadama*			small new year, *abo/hibo*	
Ruler	tax		rice, *tonoamamu* (*Ainu*)	rice			
City people	not cultivate		rice				
Farmer	cultivate	wheat, barley				millets, *shiruamamu* (*Ainu*)	
Livestock	feeding		culm and weed, wild			culm of Japanese barnyard millet	
Wild animal	predation	wild animals and plants					

History of processing tools

Traditionally, six species have been cultivated, comprising five annual millets—foxtail millet, common millet, finger millet, Japanese barnyard millet, and sorghum—as well as the perennial Job's tear, which stands as an exception among mostly annual C4 self-fertilizing plants. Notably, Japanese barnyard, foxtail, and common millets were grown during the Jomon period, dating back several thousand years in the Japanese Archipelago.

Eight of these species, specifically foxtail millet, common millet, sorghum, Job's tear, barley, maize, rice (Poaceae), and amaranths (Amaranthaceae), possess waxy varieties. The domestication process of Japanese barnyard millet may have occurred in northern Japan following the Holocene epoch. Archaeological evidence, such as ancient pottery, indicates that soybean and azuki been seeds were present inside these vessels.

During the early *Yayoi* period, which succeeded the final *Jomon* period, ancestors cultivated rice in primitive paddy fields and foxtail millet on mounds concurrently at the Nabatake Ruins, approximately 900 BC. Even today, a few farmers continue to cultivate Japanese barnyard millet in both upland and lowland fields in northern Japan, while others cultivate it on burnt field in the southern regions.

The cultivating system for finger millet in Yamanashi, Central Japan, mirrors that of Karnataka, India; in both regions, farmers transplant finger millet seedlings from nurseries. Villagers in these areas have preserved numerous local millet varieties, with the region renowned for the longevity and good health of its inhabitants.

The local communities have developed and practices a variety of cookery techniques, utilizing taro, millets, barley, wheat, and rice. This culinary style demonstrates notable similarities between Japan and India.

Nakao (1967) described the basic agricultural complex as "to stomach from seeds," consisting of diverse elements such as tools and methods (Figure 80). The complexity of these systems also embraced the intelligence and skills inherent in each individual (Figure 81).

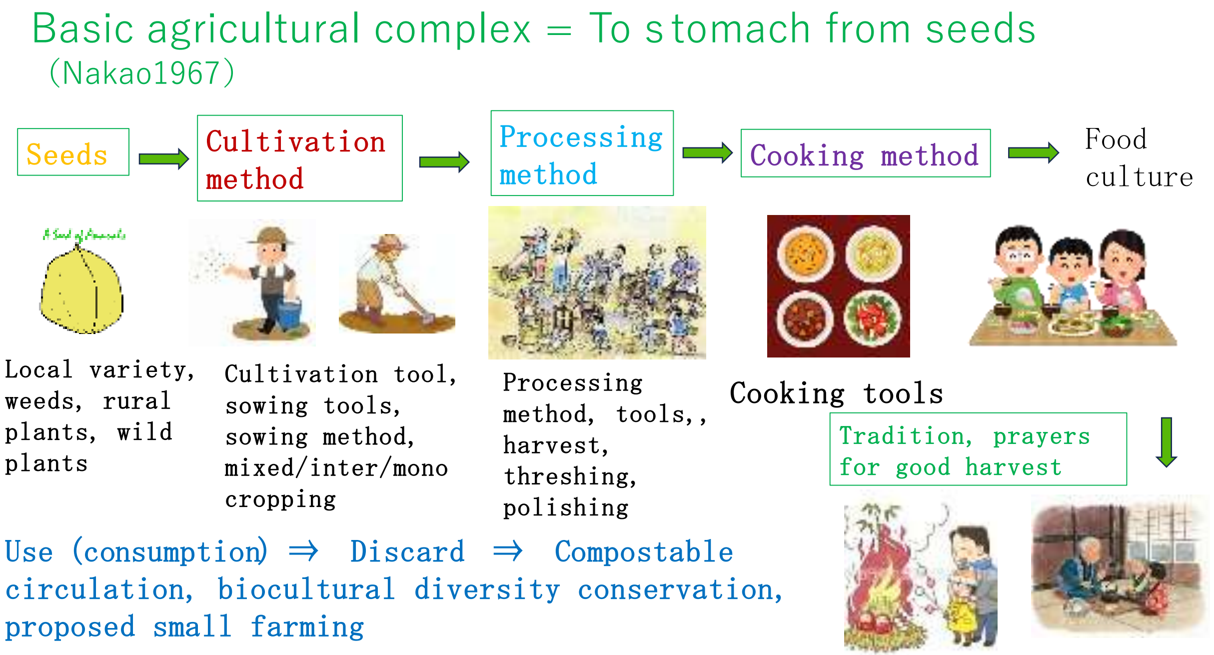

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Figure 80. Basic agricultural complex

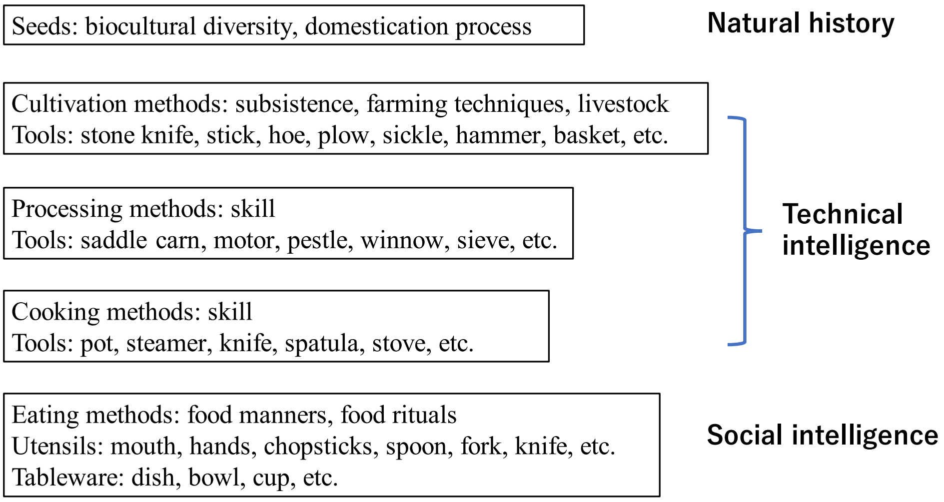


Figure 81. Natural and artificial evolution of tools and methods

The evolution of processing tools is depicted historically in Figure 82 (Kimata 2025, Miwa 1989, Nakao 1967). Humans have continually developed and utilized a wide variety of tools to support daily life. Civilization has advanced through three main interventions: fire, tools, and language. In creating tools, people have used natural materials such as water, water, wind, stone, soil, wood, and metal. These materials have been essential in processing grains and other foods. While tools and machines have become increasingly efficient, their underlying mechanisms have remained fundamentally unchanged.

In ancient Japan, people used many tools crafted from stone, soil, and wood (Figure 83). Clay pots from the middle *Jomon* period (Katsusaka-style of Central Japan) have been found to contain soybeans and azuki beans, dating back to approximately 5000 BP (Nasu 2018).

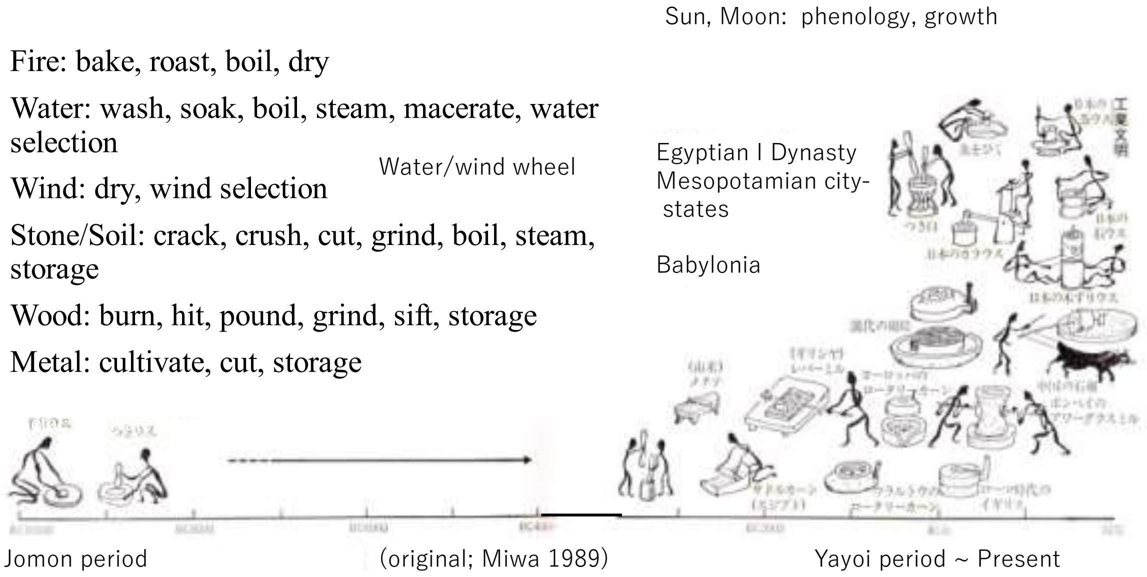


Figure 82. History of grain-processing tools

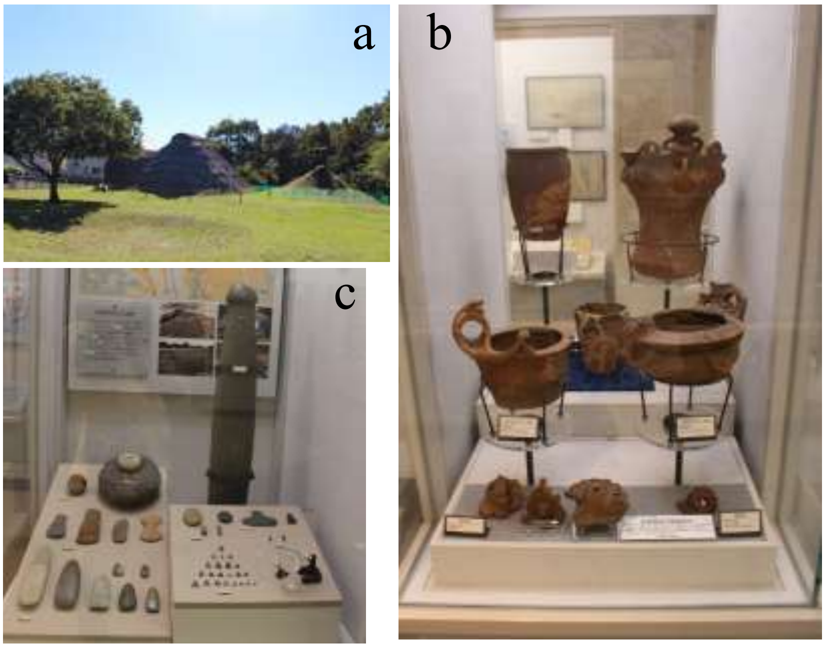


Figure 83. Tools excavated at the Katsusaka Jomon ruins
a, Village; b, stone tools; c, clay pots.

The agricultural tools utilized by Indian farmers are depicted in Figures 84–86. Even in contemporary times, many farmers in rural areas continue to use these traditional tools. In contrast, large-scale agriculture in India has adopted mechanized methods similar to those used in the United States, particularly since the advent of the Green Revolution.

Local farmers make use of a variety of farming tools for daily agricultural activities. Seeds are commonly sown in rows. Traditionally, threshing was accomplished by having animals tread on thee harvested crops. In modern practice, threshing is sometimes performed using cars driven over the crops, as illustrated in Figure 84. Grains are ground into flour using millstones, which closely resemble the ancient saddle quern (Figure 85). In addition, housewives possess and maintain a range of cooking tools, regularly polishing them for use (Figure 86).

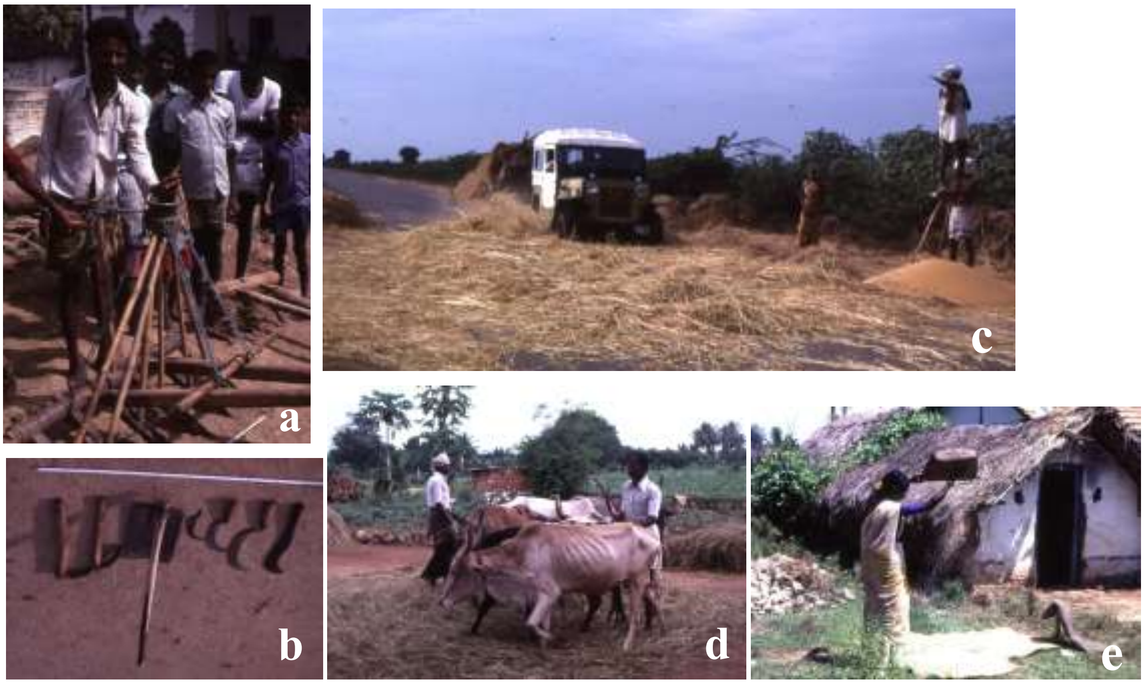


Figure 84. Tools for cultivation and processing

a, Sowing tool; b, cultivating tools; c, threshing on the road; d, threshing by cow stepping pressure; e, wind selection by winnowing basket.

Figure 85. Milling tools

a, Millstone for finger millet in Karnataka, India; b, saddle quern excavated at the Katsusaka Jomon ruins in Japan

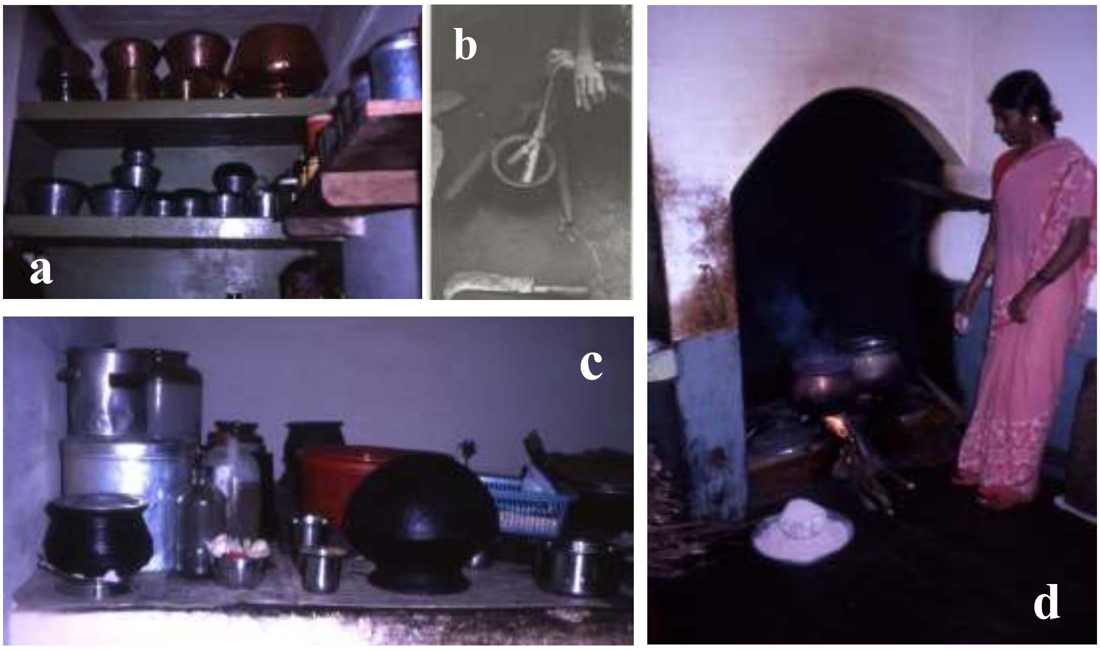


Figure 86. Kitchen utensils
a, Pots; b, kneading pin for *mude* and cooking knife; c, pots and cups; d, stove.

Processing of millets and the faith in Japan

In Japan, the use of traditional motors for processing grains has become rare, even in mountain villages (Figure 87). Farmers have historically hulled, polished, and milled grains to produce powder, and then pounded waxy rice to make *mochi* and soybeans to make *miso*. Notably, a key difference exists between Japanese and Indian waterwheels: the Japanese version rotates vertically, while its Indian counterpart rotates horizontally.

Agricultural rituals have been preserved and handed down through generations (Figure 88). During the important harvest ceremony known as *niiname-sai,* held at the Imperial Palace, the Japanese Emperor offers ears of rice and foxtail millet to the ancestors. Selected farmers cultivate these crops specifically for the ceremony and present their harvest to the Emperor. Waterwheels, millstones, and wooden mortars are integral to these traditions.

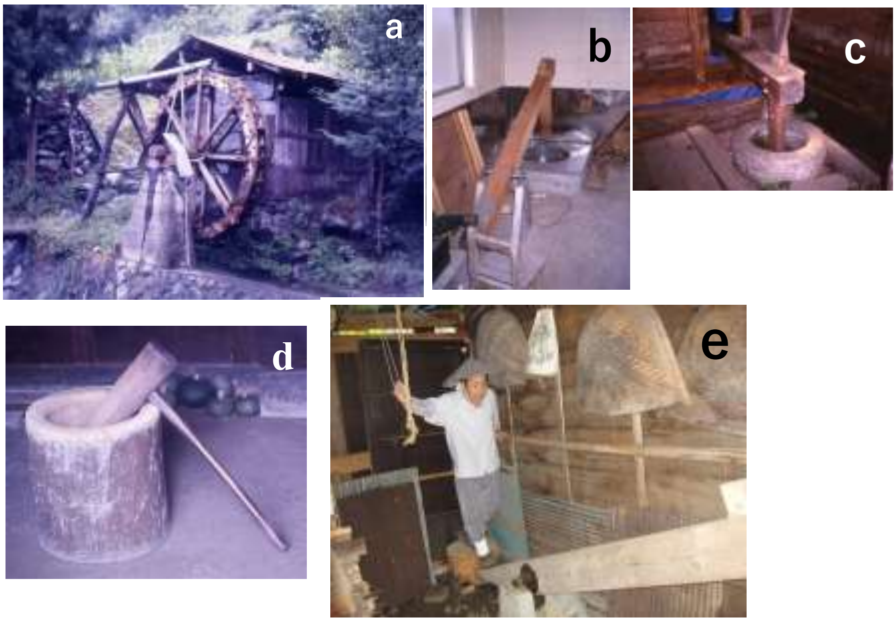


Figure 87. Processing motors in Japan

a, Waterwheel at Saihara, Yamanashi; b, stone motor at Tsushima, Nagasaki; c, at Saihara; d, wooden motor at Saihara; e, stone motor at Ikawa and Shizuoka in Japan.

Two distinctive grain processing techniques are prevalent: parboiling and wet milling. In Japan and India, farmers parboil grains—such as Japanese barnyard millet in Japan, and little millet in India—prior to de-husking. Parboiling facilitates easier removal of the husk from small grains. Subsequently, flour is produced through wet milling, which is used in everyday cooking and in offerings to deities in both countries.

Traditional festivities, such as the Little New Year, involve villagers creating figures called *kado-otoko*, decorated with spikes of foxtail and Japanese barnyard millet, as well as farm tools, straw bags, and items made from Chinese sumac (Figure 88a). These offerings are dedicated to the gods of farmers, highlighting the sacred status of certain millets like rice in Japan and India. Additionally, some communities offer a type of sushi featuring *yamame* fish stuffed with boiled grains to the *Osuwa-sama* god of hunters (Figure 88bcd). Foxtail millet is offered during the *niiname-sai*, where the Japanese Emperor offers a sacred food such as rice and foxtail millet to his ancestors in a palace ritual (Figure 88e–h).

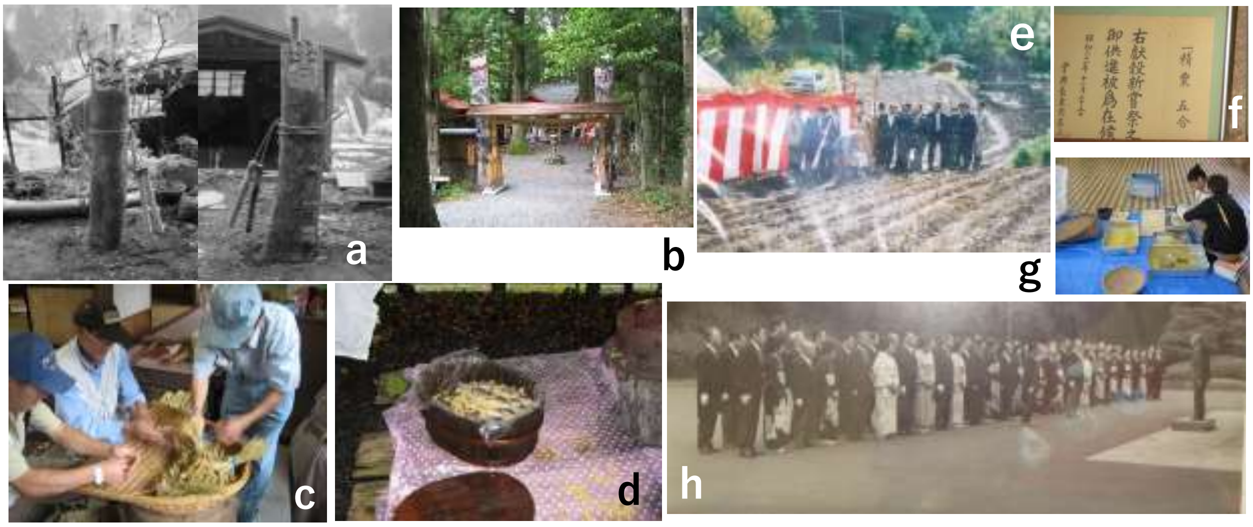


Figure 88. Agricultural rituals involving millets in Japan
a, *katsunbo* gods promise farmers good harvest in the coming autumn. They have spikes of foxtail and Japanese barnyard millet, also sickle and hoe. b, *Osuwa-sama* god shrine for hunters; c, threshing foxtail millet by hands; d, offering of a *sushi*, *yamame* fish stuffed with boiled grains, to the god. e–h, offer foxtail millet for *niiname-sai,* an important harvest ceremony held by the Japanese Emperor at Kosuge, Yamanashi pref. (1986 and 2008) and in the Imperial Palace.

Dispersal hypothesis of the agricultural complex in the Indian subcontinent

Numerous land routes traversed Central Eurasia, overcoming formidable obstacles such as the Himalayas, Takla Makan deserts, Kazakh Steppe, and various rivers and lakes (Figure 89). Early humans traveled long distances from west (Europe) to east (India and China), facilitating the spread of crops over thousands of years.

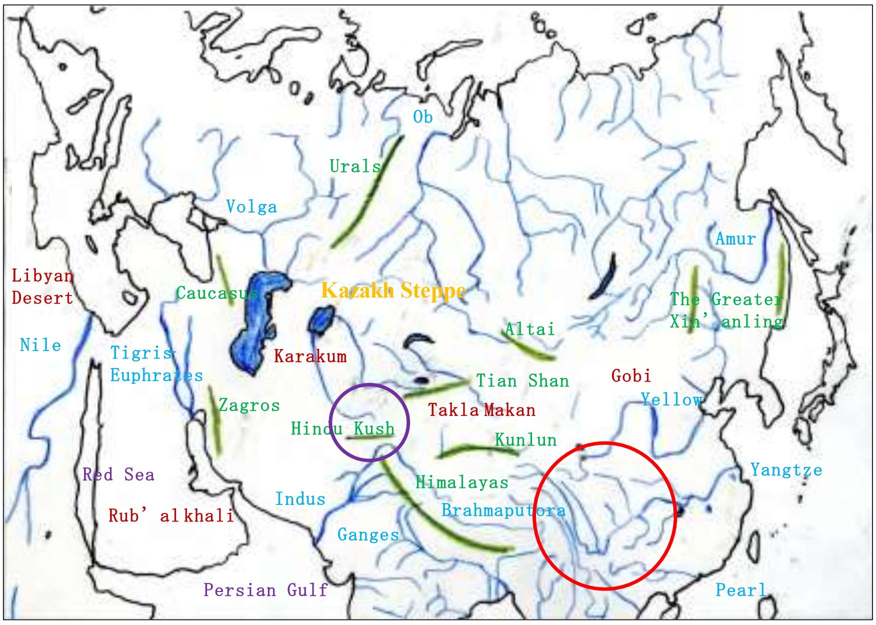


Figure 89. Mountains, rivers, and deserts in Central Eurasia

Simultaneously, ocean currents connected regions including Africa, the Indian subcontinent, Southeast Asia, the Philippines, and Japan (Figure 90). These routes enabled ancient peoples to travel and exchange crops across vast distances, with connections extending from Africa through Eurasia and across the Indian and Pacific Oceans (Oda 2017). Both land and sea routes played vital roles in the dispersal of agricultural species and practices.

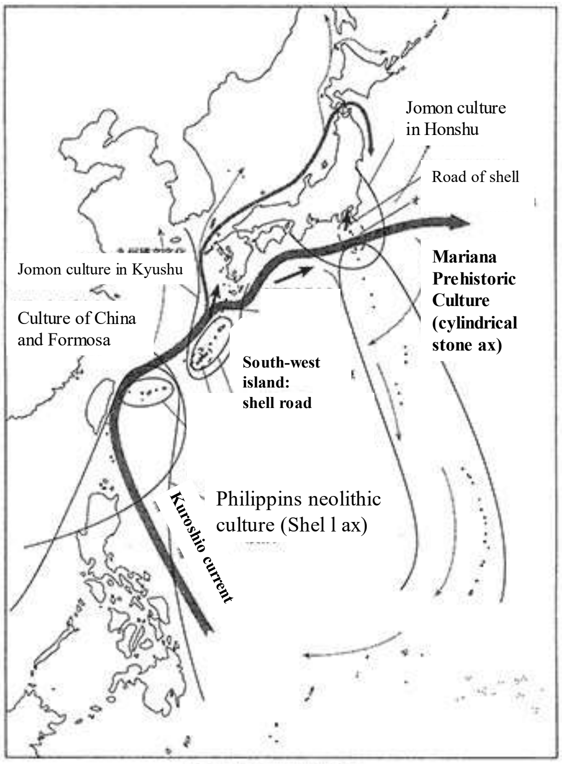


Figure 90. Ecosphere of Kuroshio Current in the Prehistoric period
(Oda 2017 modified)

Banana, sugar cane, and taro propagate primarily through vegetative propagation—using tillers, culms, and tubers or basal shoots, respectively. In contrast, wild perennial rice propagated via rhizomes and seeds in wetlands (Katayama 1987), forming the basis of vegetative planting agricultural complex. These wetlands eventually became the first paddy fields. Ancient peoples experimented with transplanting tubers, culms, and seedlings—methods later applied to rice as well.

1) According to Nakao (1967) and Sasaki (1994), the characteristics of vegetative planting agriculture include:

① No reliance on seed farming
② Utilization of polyploid crops
③ Absence of legumes and oil crops
④ Grip stick farming techniques
⑤ Transition from backyard to burnt field cultivation
⑥ Utilization of Job’s tear
⑦ Distribution of the vegetative planting culture to Africa

Based on recent knowledge, the vegetative planting agriculture complex played a significant role in the domestication of rice, a perennial wetland plant. Rice seedlings and tillers were transplanted in ways similar to banana, sugar cane, and taro in South China. As rice spread to the mountainous region of Zomia, artificial selection favored ecological annual varieties and upland rice. Upon reaching the Deccan Plateau, rice cultivation developed into an annual cropping system adapted to the monsoon. Job's tear and *kodora*, originally perennial companion weeds, were also domesticated as secondary crops.

2) Finger millet was the primary crop in the Savanna Agricultural Complex, while foxtail millet and common millet were cultivated in the arid regions from northwestern India to western Pakistan. *Kolati* (*Setaria pumila*, syn. *S. glauca*) was grown in Bombay state, and foxtail millet was first domesticated in India. Barnyard millet was domesticated in India and later spread northeast, adapting to the temperate evergreen broadleaf forests, and eventually reaching Japan.

While finger millet remained a key crop in the Savanna Agricultural Complex, evidence suggests that foxtail millet and common millet were domesticated in the steppe region at the southern base of the Tien Shan Mountains. Many millet species were domesticated in South India, with secondary crops such as *samai*, *jangora* (*Echinochloa frumentacea*), *korne*, and *korati* becoming more resilient to aridity than their mimic companion weeds in rice cultivation (Chapter 5). In contrast, Japanese barnyard millet (*hie*, *Echinochloa utilis*) was domesticated from wild annual species in northern Japan's wetlands. Rigorous weeding due to row sowing methods in the Savanna Agriculture meant that secondary crops did not originate there (Nakao 1967), but instead from mimic companion weeds in rain-fed and upland fields during the dispersal of rice from East to South India (Kobayashi 1987, 1989, 1991, Chapter 5). However, Japanese barnyard millet was domesticated during the *Jomon* period, while *E. frumentacea* was domesticated in India.

3) In the Savanna Agricultural Complex, crops differed markedly from weeds, which acted as competitors. In contrast, weeds in wheat fields were not always an antipathist enemy and often became secondary crops. However, in the Savanna Agricultural Complex, due to row sowing and thorough weeding, secondary crop development did not occur.

4) The Savanna Agricultural Complex began in dry tropical savannas, where ancestral peoples gathered wild grains of the Poaceae family during the summer monsoon. As the complex spread into wetter regions, people encountered aquatic grasses and selected wild rice among the hygrophytes. In these conditions, rice was viewed as one of the many millets grown in paddy fields. It was not necessary to distinguish rice specifically from other millets.

5) Rice domestication began in India as part of the Savanna Agriculture Complex; thus, rice was originally regarded as one of the millets. Rice was cultivated in paddy fields on the plains, and later, upland rice varieties were developed in the Assam mountains as cultivation spread westward.

6) Rice and finger millet transplantation practices also evolved. Farmers in South India (Figure 91) transplanted finger millet, a practice that extended to Nepal (including even Japan on upland field). While finger millet was usually sown directly, transplantation during the July monsoon ensured healthy root establishment, even in upland fields. The transplantation of rice was initially thought to mimic that of finger millet, particularly in Bihar, East India (Figure 91). However, later evidence suggests that the transplantation of finger millet was, in fact, modelled after the rice method.

Figure91. Finger millet cultivation practice

a, Nursery; b/c, transplanting in paddy fields; d, harvesting by ear cutting.

7) The Assam mountains and Zomia represented a significant region within the Vegetative Planting Agriculture Complex, where the primary agricultural focus was on the cultivation of tubers. When farmers in this area were introduced to a new crop like upland rice, they adapted their traditional agricultural methods to accommodate it. Using *hori* sticks, which were tools originally employed for dot-spreading tubers, they began to cultivate upland rice in a similar fashion. As a result, upland rice achieved comparable status to foxtail and common millets within their agricultural systems. This introduction was accompanied by the cultivation of waxy varieties of Job' tear. Notably, these cereals—upland rice, foxtail millet, common millet, and Job's tear—were annuals, though is some cases, they could be considered perennial in their ecological behavior.

8) Harvesting immature grains from wild grasses posed challenges due to their high moisture content, which made them unsuitable for storage. Thus, farmers were forced to either consume these grains immediately or process them to extend their usability. One common solution was the parboiling method, which was commonly practiced in India to produce chiura (beaten rice). Similarly, in Japan, parboiling method (*shiromushi*/*kuromushi* methods) were applied to Japanese barnyard millet, allowing these grains to be processed for later use.

Major revision on the Vegetative Planting Agriculture Complex

A comprehensive reassessment of the Vegetative Planting Agricultural Complex is necessary particularly in light of the considerable body for research published since Nakao's hypothesis (1967). Nearly 60 years have passed, and significant progress has been made in understanding the origins and development of agriculture. As such it is essential to reconsider and reexamine the eight key issues previously outlined.

The dispersal routes of bananas and rice overlapped significantly in South China and Zomia (Figures 92–94) (Bellwood 2005). Within these regions, the Rice Agricultural Complex emerged as an advanced agricultural system. Bananas, as large, stooling herbaceous perennials, are propagated vegetatively through corms (Eguchi 1958). The domestication of the typical seedless edible banana was driven by two evolutionary processes: parthenocarpy and sterility. Edibility first evolved in wild *Musa acuminata*, a highly variable in nature, with the Malay Peninsula identified as its primary center of diversity (Simmonds 1995).

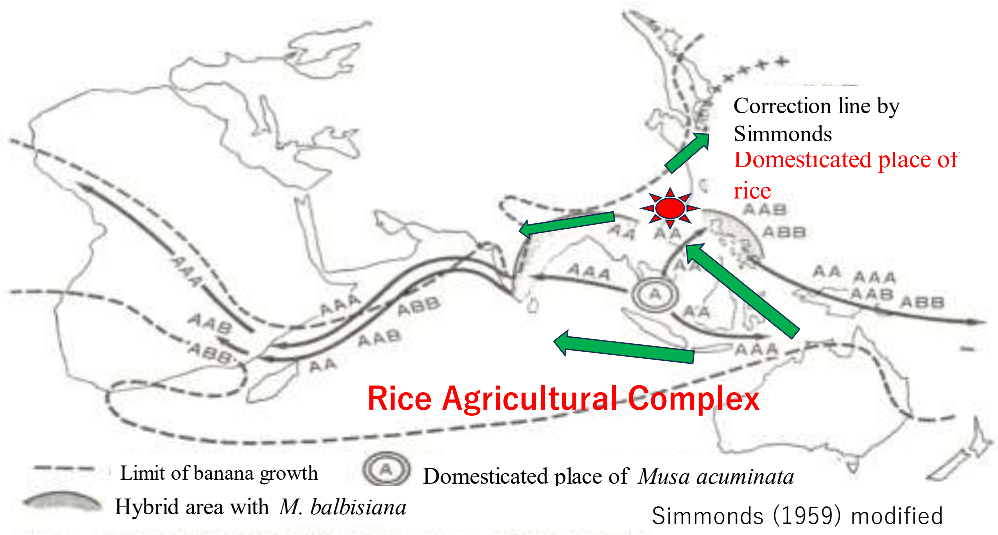


Figure 92. Origins and distribution of bananas and the Rice Agricultural Complex

Sugar cane, another important perennial grass, is cultivated through stem cuttings and is typically harvested approximately one year after planting, with subsequent ratoon crops collected annually until yield declines necessitate replanting. Originating in the tropics, sugar cane's geographic range was extended through interspecific hybridization, principally with the wild species *Saccharum spontaneum*, the most primitive *Saccharum* species believed to have evolved in the Himalayan foothills of northern India. The dispersal of *Saccharum officinarum* to the east across the Pacific and northwest, along with somatic mutation, contributed to its increased diversity (Roach 1995).

The coconut palm is a key crop throughout the humid tropics, flourishing at altitudes up to 600 m. While the palm can grow in drier climates and higher altitudes, it does not fruit as well in these conditions. It is likely that early human populations settled in coastal and island regions where wild coconuts already existed. Approximately 3000 years ago, the progenitors of the Polynesians left the Melanesian region by boat, spreading into the Pacific and Indian Oceans (Harries 1995).

In the Yang-shao culture of China, rice cultivation began later than that of foxtail millet and likely after panic (syn. common) millet. Similarly, in India's Harappan civilization, rice was domesticated later than wheat and barley. In the wet tropics of Southeast Asia, rice was introduced after an original agricultural system founded on taro, yams, banana, Coix (syn. Job's tear), and various other crops. Both upland and swamp rice invaded the southeastern monsoon belt, gradually replacing agriculture based on roots and tree crops. Notably, taro was cultivated as a wet-field crop long before the arrival of rice in the area. Farmers constructed terraces and channeled water to them for taro cultivation. It has been suggested that rice may have been domesticated from weedy races infesting wet-field taro plantations. However, there is currently no definitive evidence to confirm or refute this theory, and it is likely that this process, if it occurred, was supplementary to the domestication of rice in the savanna zones. Over time, rice became woven into the religious and cultural practices of rice-eating communities. For example, many Hindus prefer wild rice as an offering in temples over cultivated rice. Indeed, rice cakes, rice balls, rice wine, rice flour, and whole-grain rice are all used as offerings of thanks (Harlan 1977).

Even today, crops such as banana, sugar cane, taro, and coconut palm are commonly grown on nearby wet-fields (Figures 93 and 94). Taro is one of the world's oldest food crops, dating back over 9,000 years and is considered an orphan crop—locally significant but not widely traded as an international commodity and thus attracting limited research attention (Rao et. al., 2010). Taro's importance is particularly apparent at the community level, where, with the exception of its skin, all parts of the plant are edible.

Beyond its nutritional value, taro holds sacred status in many cultures, imbued with high prestige and strong symbolic significance. In the Pacific, taro is presented on formal occasions, agricultural rituals, and religious celebrations. Alongside dalo (syn. taro), farmers and community members maintain a diverse array of crops, including breadfruit, bananas, plantain, coconut, yams, wild yams, giant taro, and sugar cane. The experiential and educational dimensions of agritourism enterprises extend beyond tourist engagement, with the long-term success of biodiversity conservation programs dependent on empowering local communities to take ownership and management responsibility (Berno 2020, Hunter et al. ed. 2020).

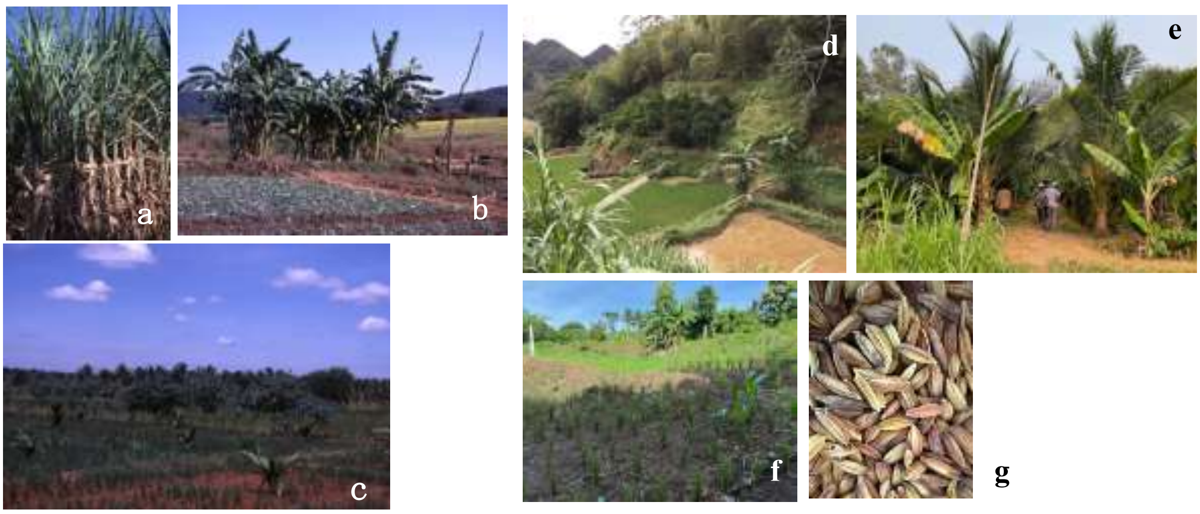


Figure 93. Sugar cane, taro, and banana grown near rice paddy fields in Eastern India.
a, Sugar cane; b, banana; c, coconut palm in eastern India. d, paddy fields near banana; e, coconut palm and taro in Vietnam; f, paddy fields near banana; g, traditional variety of rice in Thailand (photographs by M. Ino and K. Nakagomi 2025)

Common millet serves as a versatile food crop with a variety of culinary applications. In Eurasia, it is used to prepare boiled grains, waxy dumpling *mochi*, non-waxy gruel. These diverse preparations reflect the significance of millet in regional diets and its adaptability to different cooking methods. Ethnobotanical studies discussed in Chapter 4 indicate that common millet was likely cultivated first in Central Asia before dispersing to Europe and China before 6500 BC. Over time, several millet species—finger, common, foxtail millet—spread as far as Southeast Asia. Notably, East Asian cultures historically favored waxy foods made from cereals.

In the Northern Philippines, rice holds a central place in daily meals and cultural rituals. Boiled rice (*hinamal*) is a staple of traditional meals, while fermented glutinous (waxy) varieties are used to produce rice beer (*bavah*), which plays an essential role in ritual and special social occasions. Meals typically feature a starchy staple (*anon*), preferably rice. Other boiled grains or root crops (most frequently sweet potato tubers, *lapne*) may substitute for rice. The region's starch staples include rice (non-waxy, 82%), sweet potato (30%), taro (3%), and others, including millet. Historically, terracing for rice and taro cultivation, alongside shifting cultivation of yams, taro, and other root crops (excluding sweet potato), as well as millet and sorghum, was practiced in all the major Ifugao valleys. Before the widespread adoption of sweet potato in the 16th century, gentle sloping valleys likely attracted small populations of shifting cultivators who utilized pond-field terracing for taro. The introduction of sweet potato accelerated both agricultural and demographic changes (Conklin 1980).

Millets had been dispersed from mainland Asia to the Sunda islands (Figure 94a) (Kano 1946 modified by Kimata), although Japanese barnyard millet did not reach this region. Seven species are known to have waxy varieties: rice, foxtail millet, common millet, sorghum, Job' tear, maize, and barley. Unlike these, Japanese barnyard millet traditionally lacks a waxy variety. Waxy grains are characterized by a sticky texture (*mochi*) similar to that found in vegetative planting cultures using banana, taro, and yam. Southeast Asian populations favored sticky-textured foods, leading to the development of biocultural diversity in cereal domestication under the influence of the Vegetative Planting Culture (Figure 94b) (Sakamoto 1989).

Raw consumption is possible for certain crops, such as yam (tubers), banana (fruits), and sugarcane (culms). In contrast, taro and grains require cooking methods involving heat, such as boiling or baking to be edible.

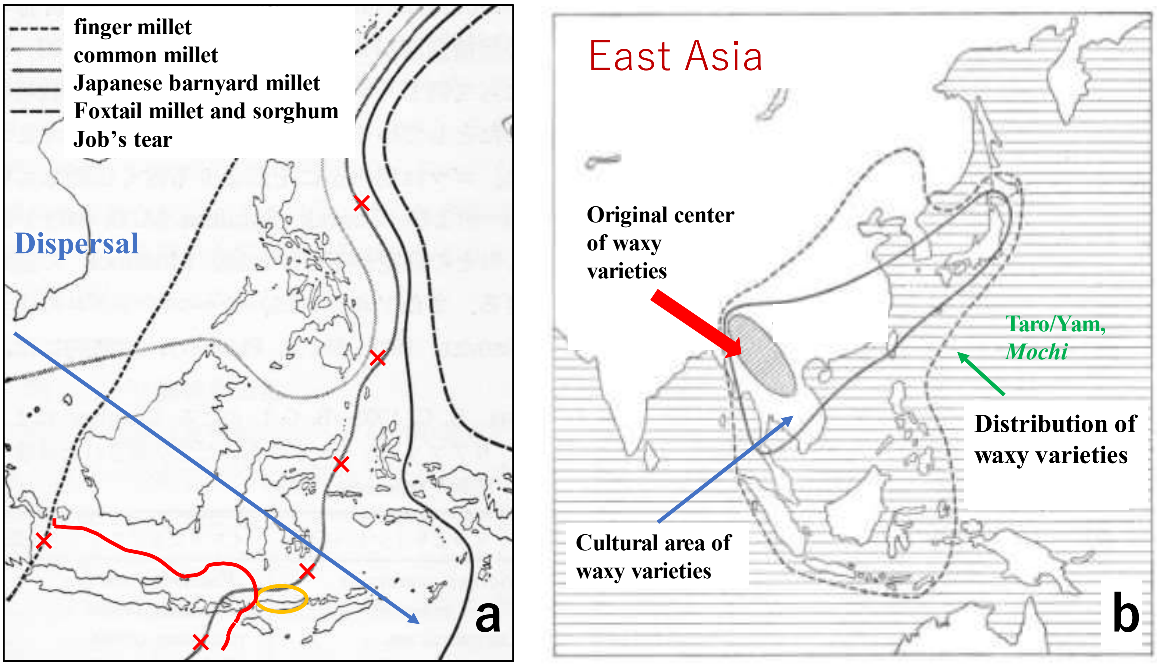


Figure 94. Dispersal of millets and waxy varieties across Southeastern Asia

a, Kano (1946) modified; b, Sakamoto (1989) modified

A comparative linguistics study between Tamil and Japanese (Table 52) conducted by Oono (2000) identified numerous similarities in farming and food processing terminology. Oono (2004) posited that these terms spread from Tamil to South Japan during the early *Yayoi* period (Figure 23), suggesting cultural and agricultural exchanges. Oono also theorized that rice and foxtail millet cultivation reached Japan from Tamil via ocean currents during this period.

Oono had presented as follows: in Yayoi period (800 BC-AD250), Tami language had dispersed to Japan, and then the partial Tamil words especially on farming and in Megalithic age (1000 BC-AD 300), had accepted as creole. The cultural characteristics had been shown ; ①steel manufacturing technology, ②megalithic tomb, ③earthenware, ④cultivated fox millet on upland and rice in paddy fields, ⑤prayers for good harvest, and ⑥possession. Oono had compared with the ancient Japanese culture and the Tamil culture, based on the classic poetry collection *Sangam.*

Table 52. Comparison of farming terms between Tamil and ancient Japanese

English	Tamil	Ancient Japanese	Today Kanji
levee	acc-u, kur-ampu	az-e, kur-o	畔
bund	an-ai	un-e	畝
paddy field	vayal, tampal	tamb-o	水田
field	pat-ukar	fat-ake	畑
slash-and burn cultivation	kum-ari	kob-a	焼畑
mountain fermland	puravu		山の畑
foxtail mille	av-ai, tinai, enal	af-a	粟
rice	nel、enal	sin-e, ina, ine, nel	稲
paddy rice	pu	fo	水稲
rice grains	nel	ni	稲粒
rice offered to a god	kum-ai	kum-a	供米
bran	nukk-u	nuk-a	糠
boiled rice	arici	meshi	米飯
shitogi	cit-ai	sit-ogi	粢
mochi	mot-akam	mot-ifi	餅
mochi flour	ar-ai	ar-e	餅粉
porridge	kal-i	kay-u	粥
loose porridge	amp-ali	am-ari	ゆるい粥
parched rice	pori		炒り米
residue	kat-i	kas-u	糟

Nakao (1976) proposed a hypothesis regarding the systematic development of agriculture complexes in Eastern Asia (Figure 96), identifying four distinctive features of the millet agriculture complex: 1) Farmers cultivated annual crops, without tubers; 2) a wide variety of legumes was grown; 3) melons and fruit vegetables were included in crop rotation; and 4) oil crops were included in the cultivation system. This system promoted nutritional balance by incorporating multiple crop types.

Sasaki (1994) summarized Nakao' theory, noting that grains were indispensable for processing, utilizing tools such as clay pots, saddle querns, wood motors, pestles, etc. (Figures 80–88). Due to the need for careful weeding, companion weeds were absent from millet fields, preventing the domestication of secondary crops. Additionally, the millet agriculture complex was not conducive to large-scale field development. Rice, treated as one among several millets in wetland cultivation, was part of the Svanna Agriculture and influenced by vegetative planting traditions. Consequently, a distinct rice agricultural complex did not emerge.

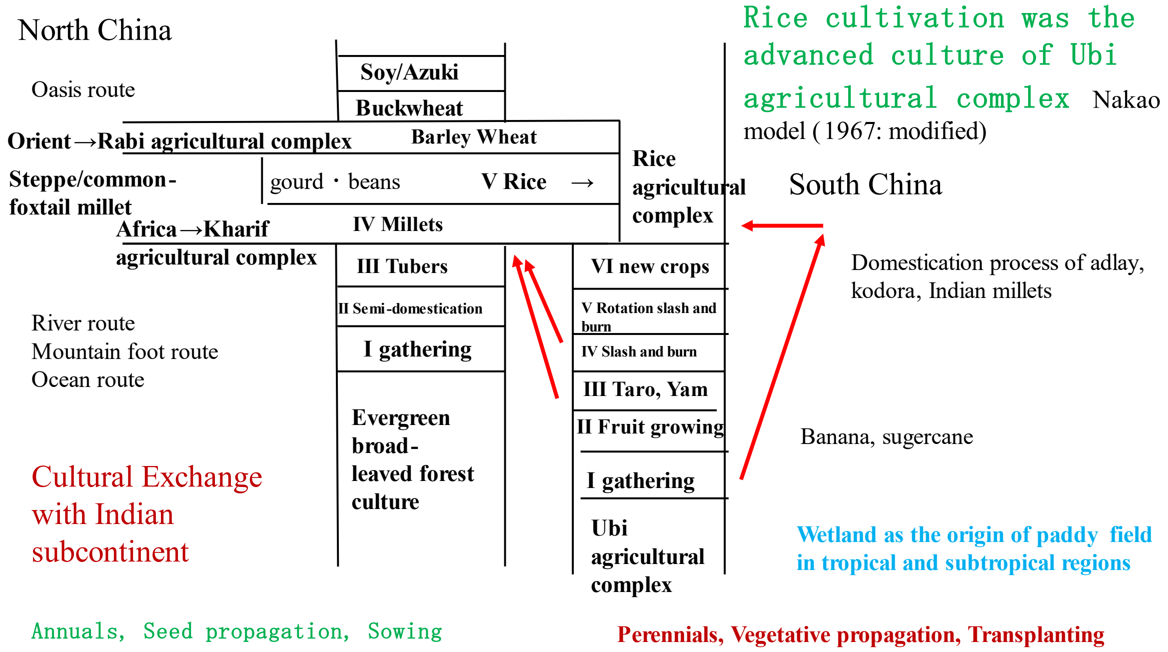
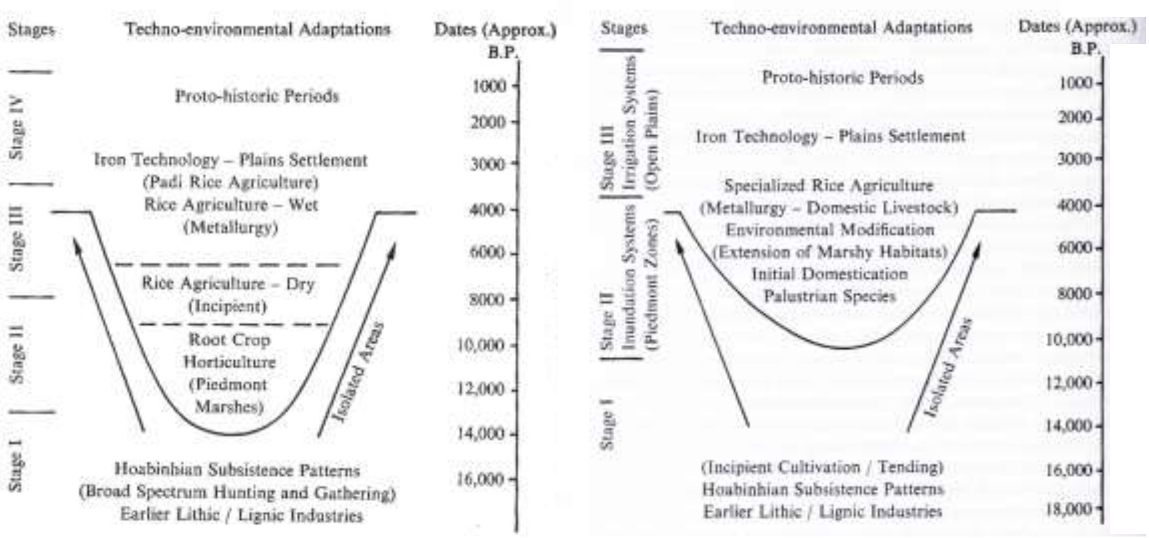


Figure 96. Development of agriculture complexes in Eastern Asia

Sasaki (1994) refuted the notion that rice and taro were domesticated within the same wetland, a theory supported by some European researchers (Saur 1952, Werth 1954, Harlan 1977, Gorman 1977, Conklin 1980). For example, Gorman (1977) proposed two models for the development of rice agriculture. In Stage II of Figure 97a, the root crop horticulture phase is a postulated reconstruction, believed to have continued until rice cultivation became sufficiently to successful to replace root crop horticulture as the primary subsistence strategy. This initial rice cultivation is thought to have adapted to lower piedmont regions, with further settlement into central plains taking place following the advent of iron technology.

In Figure 97B, an alternative view suggests rice and root crops (primarily taro and yams) were "sister domesticates," jointly domesticated before 9000 BP in palustrine zones, likely in piedmont areas of mainland Southeast Asia. Both models regard dry rice as a later adaptation, dependent on the initial domestication of wet rice. The precise timing of this secondary adaptation to swidden agriculture remains unclear. The introduction of adzes and ceramics into upland Hoabinhian sequences may reflect this upland adaptation. These models remain speculative but frame the current understanding of rice and root crop domestication.

Recent research from Southeast Asia supports a stage-based division of the second model, with the first stage marked by the initial domestication of palustrine species (e.g., taro and rice). This led to a shift in settlement patterns from upland regions to piedmont zones, where productive agricultural habitats could be more easily developed.



A: **Gorman model I (1977)** **B:** **Gorman model II**

Figure 97. Models for rice agriculture development

Direct evidence for the early evolution of cultivated rice is fragmented and sometimes controversial. While many researchers argue the Indian subcontinent is the ancestral home of *Oryza sativa*, the earliest archaeological evidence from India dates only to 2500 BC. In contrast, Neolithic rice remains in China have been dated to 8500 BP, and written records of rice cultivation in China begin in the third millennium BC (Chang 1995). Given recent findings, Nakao's hypothesis requires revision, particularly regarding the domestication sites. Over the past sixty years, research has shifted the proposed domestication center from Bihar (India), through the Yunnan-Guizhou Plateau and Yangtze River (China), to the Pearl River (China).

A new model for rice agriculture development (Figure 98) suggests that wild rice, originally a perennial species in wetlands, reproduced both vegetatively and sexually. Early peoples collected wild rice grains for food. Rice was domesticated around the Pearl River, evolving into an annual crop propagated mainly by seedling transplantation. The original wetlands became paddy fields, and rice cultivation spread to mountainous regions of Zomia and Eastern India, where upland rice was grown.

As rice reached the Eastern Ghats in India, various millets were domesticated from companion and mimic weeds (Figure 99). The detailed domestication processes are discussed further in Chapter 5.

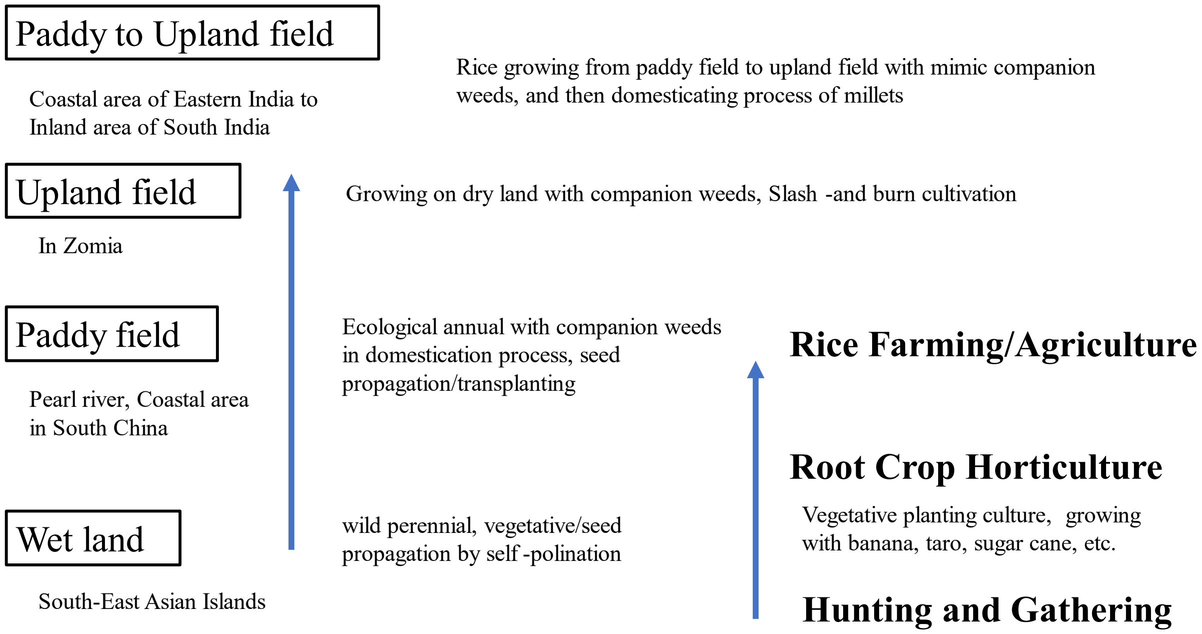


Figure 98. A new model for rice agriculture development

Comparison among the primary, secondary, and tertiary crops

Our team conducted a comprehensive study on the domestication processes and dispersal routes of Indian millets, focusing on a comparative analysis of primary, secondary, and tertiary crops. The domestication pathways of these crops were examined to highlight their evolutionary progression, ecological adaptation, and agricultural significance in the Indian subcontinent (Table 53).

Primary crops, such as common millet, were domesticated directly from wild plants. Secondary crops, including little millet (*Panicum sumatrense*), originated from companion weeds that developed adaptations for specific environmental conditions—such as cold tolerance in oats and rye and drought tolerance in millets. Tertiary crops, exemplified by korati (*Setaria pumila*), resulted from further domestication, often involving mimic companion weed types associated with other millets and upland rice.

Common millet was domesticated around 8500–8000 BP and dispersed widely across Eurasia. Little millet's domestication occurred around 4000 BP, followed by *korati* at approximately 3800 BP. All three species are annual C_4 plants. The ancestor of common millet is inferred to be *Panicum miliaceum* ssp. *ruderale*, with current populations found in regions such as the Tianshan mountains and the Kazakh steppe, areas characterized by grasslands and moderate precipitation.

Common millet exhibited broad dispersal and diverse vernacular names and cooking methods throughout Eurasia, while little millet and *korati* displayed more limited vernacular diversity and regionally concentrated cultivation practices. Little millet's wild ancestor grows in Indian wetlands, and *korati*, though cosmopolitan as a weed, is limited in its domesticated form to specific habitats such as sparse forest floors. Both secondary and tertiary crops are typically cultivated in polyculture systems and often processed together.

Table 53. Comparison among the primary (common millet), secondary (little millet), and tertiary (*korati*) crops

Cracteristics	*Panicum miliaceum*		*Panicum sumatrense*		*Setaria pumila*	
	present	**process**	**present**	**process**	**present**	**process**
	Main crop		**Secondary crop**		**Tertiary crop**	
Wild type	presence	existed	presence	existed	presence	existed
Population size	big	greater	small	small	small	small
Number of seeds	more	many	more	many	a few	a few
Gathering and use	feed	grain, feed	existed	a few	a few	a few
Weedy type	presence	shattering	presence	shattering	presence	shattering
Mimic weed type to different local crop	absent	shattering	presence	shattering	presence	shattering
Mimic weed type to same local crop	rarely	shattering	presence	shattering	presence	shattering
Hybridization between crop and mimic weed	rarely		always		always	
Mixed cropping with different local crop	rarely		presence		always	
Harvesting with different local crops	absent		presence		always	
Cooking with different local crops	rarely		rarely		always	
Distribution area of domesticated and wild types	world-wide	steppe in Eurasia	around India		part of South India	Eurasia
Diversity and distribution of local names	world-wide	Central Asia	Indian subcontinent	East India	limited area in India	South India

Kodora (*Paspalum scrobiculatum*) was domesticated in about 2000 BC and is cultivated throughout the Indian subcontinent, but mainly in Madhya Pradesh. Studies comparing ecological and morphological traits among various accessions, including weed forms, revealed a shift from perennial to ecological annual growth and the acquisition of crop-like characteristics through rice cultivation. Genetic analyses divided cultivated accessions into northern and southern groups, with northern accessions closely related to weeds from Orissa upland rice fields and southern accessions showing relationships to both local weeds and those from southern India. Two hypotheses for *kodora*'s origin have been proposed: a single domestication in Orissa followed by dispersal, or independent domestications in Orissa and southern India.

Jangora (Echinochloa furumentacea) is cultivated as food, fodder, and an emergency crop across India, Nepal, and Pakistan. Its ancestor, *Echinochloa colona*, is a common paddy field weed. Morphological and genetic studies suggest Bihar as the place of origin, with subsequent dispersal to Tamil Nadu via Karnataka.

Samai (Panicum sumatrense) is grown for food and fodder in India, Nepal, Sri Lanka, and Myanmar. Its wild ancestor, *Panicum sumatrense* subsp. *psilopodium,* also grows in paddy fields. Research indicates Eastern India as the place of origin, with distribution extending to Southern India.

Korne (Brachiaria ramosa) is cultivated extensively in India, with its ancestor found in paddy fields. Genetic and morphological studies indicate its origin in southern Orissa, followed by dispersal to the Deccan Plateau via Tamil Nadu.

Korati (Setaria pumila) is a cosmopolitan weed, but its domesticated form is primarily grown in mixed cropping systems with *kodora* or *samai* in India. The details of its domestication are discussed elsewhere in the document.

The domestication of Indian millets, based on field observations, experiments, and linguistic analysis, reveals a complex process involving secondary origins via weed and mimic companion weed types. Secondary crops such as oats and rye (in wheat cultivation) developed cold tolerance, while Indian millets evolved drought tolerance alongside upland rice. *Brachiaria ramosa* demonstrates greater drought tolerance than *Setaria pumila*, becoming an independent crop, while *Setaria pumila* is typically grown with little millet but can be cultivated alone in severe drought conditions. Both are categorized as tertiary crops, serving as double secondary crops to other millets and upland rice.

The millet domestication process highlights the significance of weed–crop complexes and the broader agricultural basic complex, reflecting a symbiotic relationship between plants and humans.

The integrating hypothesis for the dispersal route of Indian millets is illustrated in Fig. 99 on the basis of the results. *Echinochloa furumentacea*, *Panicum sumatrense*, and *Paspalum scurobiculatum* were secondary crops to upland rice. First, their ancestral plants were companion weeds derived from the relative weeds that invaded paddy fields in humid regions of Eastern India. Second, the companion weeds became insurance crops in upland rice fields, and they spread to a dry region in the Deccan Plateau (Kobayashi 1987, 1989). *Brachiaria ramosa* and *Setaria pumila* were so called 'tertiary crops' because they were secondary crops to other millet species domesticated from their relative weeds in upland fields. On the other hand, *Digitaria cruciata* has been recently derived from the relative weed grown in maize or vegetable fields, Kashi Hill, Meghalaya, and is limited to the same area (Singh and Arora 1972).

Tentatively, Indian millet species were domesticated in the process of diffusion from humid paddy fields in Eastern India to dry upland rice fields in the Deccan Plateau, Southern India.

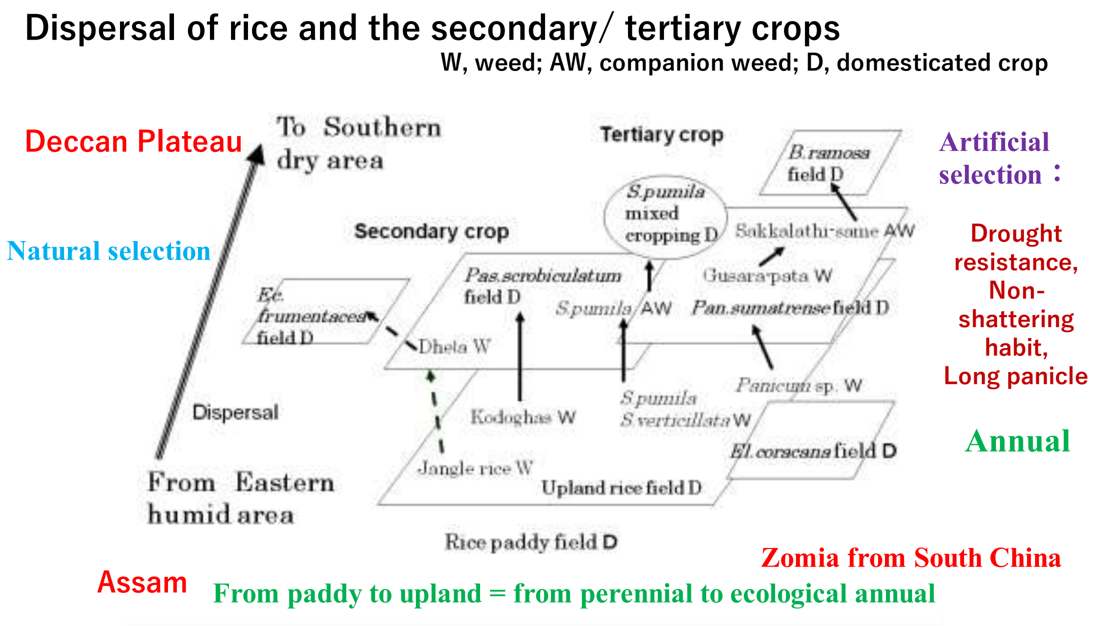


Figure 99. Model of rice dispersal and domestication through secondary/tertiary crops in the Indian subcontinent

Domestication process of millets and dispersal route in The Indian subcontinent

The domestication of millets in the Indian subcontinent has been elucidated through comprehensive field observations (Kimata et al. 2000), experimental studies (Kimata 2015a, 2015b), and linguistic research (Figure 99). The primary center for millet domestication spans the Eastern Ghats and Southern Deccan Plateau. Although the process involves complex relationships among various millet species and their relatives, the concept of secondary origin via weed and mimic companion weed types provides a valuable framework for understanding how domestication unfolded.

Analogous to oats and rye, which arose as secondary crops of wheat and developed cold tolerance (Vavilov 1926), Indian millets emerged as secondary crops of upland rice, evolving drought tolerance. *Brachiaria ramosa* demonstrates superior drought resilience compared to *Setaria pumila* and has consequently become an independent crop. *Setaria pumila* is typically grown alongside little millet but can thrive independently when little millet fails during severe droughts. Both *Brachiaria ramosa* and *Setaria pumila* are regarded as tertiary crops, serving as double secondary crops for other millets and upland rice. This domestication pathway emphasizes the critical role of weed–crop complexes and broader agricultural complexes, illustrating the symbiotic relationships between plants and human societies.

For approximately 3,500 years, indigenous millets have been cultivated throughout their present-day ranges in the Indian subcontinent (de Wet et al. 1983a; Fuller 2002; Pokharia 2008). The principal domesticated millets include *Paspalum scrobiculatum* L. (*kodora*, *kodo* millet), *Echinochloa frumentacea* Link (Indian barnyard millet), *Panicum sumatrense* Roth. (little millet), *Brachiaria ramosa* (L.) Stapf. (*korne*), *Setaria pumila* (Poir.) Roem. & Schult. (*korati*; syn. *Setaria glauca* (L.) P. Beauv.), *Digitaria cruciata* (Nees) A. Camus (*raishan*), and *Digitaria sanguinalis* (L.) Scop. (Chandra and Koppar 1990; de Wet et al. 1983a, b, c). The first three species are considered secondary in origin, having evolved through mimic and companion weeds in rain-fed paddy fields and subsequently in upland rice systems of Eastern India. The next two species, *Brachiaria ramosa* and *Setaria pumila*, were domesticated as secondary crops associated with other millets via their mimic companion weed types in South India (Kimata et al. 2000; Kimata 2015a, 2015b, Kobayashi 1987, 1989). *Digitaria cruciata* was domesticated in the late 19th century by the Kashi people in Meghalaya and now is cultivated exclusively in the Kashi Hills (Singh and Arara 1972). The origin of *Digitaria sanguinalis* remains unclear, as the species has disappeared.

While most millets, were likely domesticated in the humid regions of Eastern India, *Brachiaria ramosa* and *Setaria pumila* have adapted to the dry climate of the semi-arid tropics. *Brachiaria ramosa* was cultivated in the hot, arid red soil regions of Southern India, whereas *Setaria pumila* was grown in the hot sub-humid ecoregion with red and lateritic soils in Orissa, as well as in the hot semi-arid ecoregion with red loamy soils in Southern India (Sehgal et al. 1992). *Brachiaria ramosa* exhibits greater drought tolerance than *Setaria pumila*, having specialized for arid environments and nearly attained the tertiary domesticated phase (Kimata et al. 2000). In contrast, the local varieties of *Setaria pumila* have adapted to drier fields in Southern India compared to those in Orissa. *Setaria pumila* was typically grown with *Panicum sumatrense*, but became a stand-alone crop when the latter failed to grow in severe droughts, as observed in a 1987 survey. This adaptability suggests that *Setaria pumila* could become an independent crop. Currently, *Brachiaria ramosa* is an underutilized millet, cultivated primarily in the dry districts of Tumkur and Anantapur in Karnataka and Andhra Pradesh, respectively. It is cultivated in pure stands as a sole tertiary crop, while *Setaria pumila* continues to be cultivated through mixed cropping with *Panicum sumatrense* and other grains, remaining a minor domesticated plant.

The concept of the "agricultural basic complex," the so-called "from seeds to stomach" approach, was introduced by Nakao (1967) in studies on the origin of agriculture. A domesticated plant is invariably linked to a broader cultural complex, encompassing cultivation methods, processing, culinary practices, religious usage, vernacular names, and other cultural elements (Kimata and Sakamoto 1992).

Bellwood and Renfrew (2002) further developed the "farming/language dispersal hypothesis," integrating archaeological, linguistic, and genetic evidence from a comparative perspective. The diverse millets and their related weeds possess numerous vernacular names across different regions and languages. This analysis reconstructs the domestication process of *Brachiaria ramosa* and *Setaria pumila* from the standpoint of their vernacular names, drawing on linguistic archaeology. However, linguistic data on indigenous millets remain limited (Fuller 2002; Southworth 2005).

In light of these findings, an integrative hypothesis for the domestication process and dispersal of millets is proposed. This hypothesis synthesizes factual material gathered through fieldwork and interdisciplinary research in botany, cultural anthropology, linguistics, and archaeology, offering new insights into the complex history of millet domestication and spread throughout the Indian subcontinent.

Sakamoto (1989) identified seven primary regions of domesticated plant origins and later added Eastern India and North Japan (Figure 100).

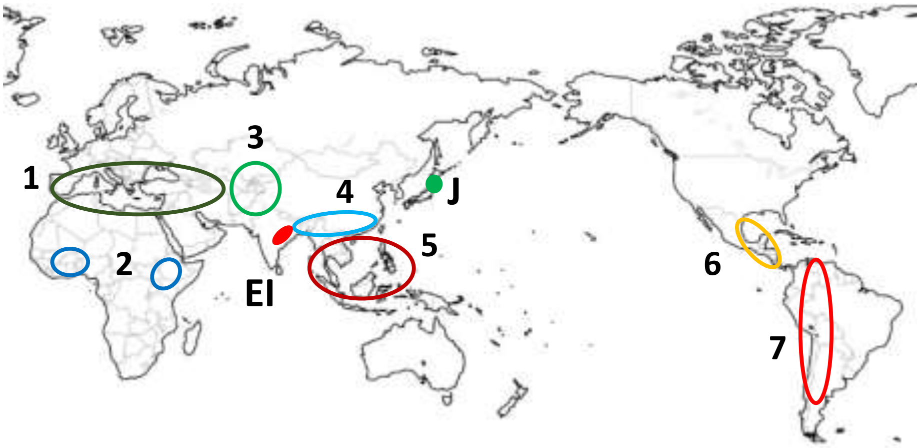


Figure 100. Six geographical origins of domesticated plants, including Central Asia, Eastern India, and North Japan

1, Mediterranean; 2, African savanna; 3, Centra Asian steppe; 4, Southern China and Zomia; 5, Southeastern Asia; 6, Central America; 7, South America; J, North Japan; El, Eastern India. (Sakamoto 1987, modified by Kimata)

Graeber and Wengrow (2021) has suggested new independent centers of domestication. Archaeological science now recognizes between fifteen and twenty such centers, each with its own distinct developmental trajectory, varying considerably from the well-documented cases of China, Peru, Mesoamerica, and Mesopotamia. Among these early farming centers, notable additions include the Indian subcontinent—where browntop millet is a key species—the grasslands West Africa, the central highlands of New Guinea (banana, taro, and yam cultivation), the tropical forests of South America, and the Eastern woodlands of North America.

To further clarify the diversity of agricultural development, the characteristics of four primary agricultural complexes and three additional systems in Afro-Eurasia have been compiled (Table 53). The four main complexes (Nakao 1967) are *Rabi* farming (mainly wheats), *Kharif* farming (African millets and yams), *Ubi* farming (tubers and banana), and New World farming (maize and tubers). The three additional agricultural systems are Nomadism in Great steppe (common millet), Indian Agricultural Complex (wheats, millets and rice), and Rice farming.

The domestication process has proven to be highly intricate, involving genetic and ecological factors (Figure 99). The geographic dispersal of domesticated crops has been extensive and has spanned a considerable period of history (Zohary and Hopf, 2000).

Proposal for an enlarged model of the agricultural complexes around the Indian subcontinent

A proposal has been made to expand the existing model of agricultural complexes around the Indian subcontinent (Table 54). Given the clarification of the original centers for rice and common millet, Nakao' hypothesis requires partial modification. First, the Indian agricultural complex is positioned at the center, and two expansive complexes are added: Nomadism in the Great Steppe and Rice Farming in the Tropics. The key features of these complexes are as follows: ① all complexes fundamentally consist of grains, beans, and oil crops. However, nomadic populations typically consume grains and daily milk products, while livestock feed on crop culms and leaves. ② the *Rabi* Agriculture Complex does not feature edible tubers. ③ Rice, Job' tear, and *kodra* are perennial plants in wetland environments, but function as ecological annuals in upland fields. ④ During the differentiation of upland rice, companion weeds resembling Indian millets were domesticated in the Eastern Ghats region. ⑤ Crops and vegetable selection has historically been determined by factors such as topography, elevation, and the time of the rainy season. ⑥ Mountainous farming systems utilize crop rotation, mixed cropping, and intercropping techniques. ⑦ Tubers are absent from the Savanna region and Great Steppe. ⑧ Sowing methods employed include broadcast, furrow, spot sowing, and transplanting. ⑨ As grain yields increased and large quantities were stored, agriculture emerged as a foundation for local economies, enabling the provision of tax grain to rulers, which in turn facilitated the formation of city-states (Scott 2017).

Table 54. Four primary agricultural complexes, along with nomadism, Indian agriculture, and rice farming

Farming format	Rabi farming	Karif farming	Nomadism	Indian Agricultural complex	Rice farming	Ubi farminng	New world farming	
	Mediterranean Agriculrural complex	Savanna Agricultural complex	Great steppe		Rice Mixed culture	Vegetative Planting Agricultural complex	Mesoamerica Agricultural complex	South America Agricultural complex
Characteristics	West Asia・Mediterranean costal are, wheat farming in winter	Africca and Indian subcontinent, Millet farming in summer	Central Eurasia, Nomadism	Complex farming accepted/ transformed from the Afro-Eurasia	Combined Ubi farmings in East and South Asia	Tubers farming in East-South Asia	Vegetative Planting Agriculture and Maze in summer	
Place of origin	Orient	Around Niger river and Eastern Africa	South mountain foot of Tienshan in Central Asia	Indian subcontinent	Southern China	around Malay peninsula	Mexiico, Mesoamerica	Andes, and flatland in East mountain foots
Distribution	Mediterranean, Orient, Afro-Asia	Sahara, Ethiopia, West India	Central Asia, Pakistan, North-Western India,Afghanistan, Iran	Inndian subcontinent, South foot of Tian Shan	East Asia, from South-East Asia to East India and Sri Lanka	Oceania, Malaysia, India and Central Africa	North America	North West of South America
Race	Caucasoid	Negroid	Caucasoid, mixed race	Mixed race, Aryan, Dolavida, Draviidian, Mongoloid, Austro-Asia	Mongoloid	Mongoloid	Mestizo	Mestizo
Environment	mediterranean climate, winter rain, flatland	sabanna climate, summer rain, flatland	steppe climate, summer rain, desert, mountain foot, oasis	savanna, steppe, tropical rain forest; flatland, hill, mountain foot	evergreen brooadleaf tree, deciduous mixed forest tree, tropical forest, flatland/wetland, flood plain, mountain	tropical rain forest	tropical rain foorest	Temperate summer rain
Crop ecology	winter annual, seed propagation	summer annual, seed propagation, vegetative propagation	summer annual, seed propagation		ecological annual, seed propagation, vegetative propagation	perennial, vegetative propagation	summer annual/seed propagation, perennial/vegetative propagation	
Major grains	wheat, barley, rye	finger millet, sorghum, pearl millet, rice	common millet, foxtail millet, oat	wheat, barley, rice, millets	rice	adlay		maize, mango
Major beans	chickpea, lentils	cowpea, kidney bean	lentils	pigeon pea, mung bean	soybean, azuki bean	pigeon pea, mung bean	kidney bean	peanut, kidney bean
Major tubers		yam		yam, taro	taro (satoimo)	yam, taro	sweet potato	cassave, potato
Major oilseeds	canola, mustard, safflower, linseed, olive	oil palm, niger seed, castor bean		mixed	mustard	coconut palm, sesame	cotton, sunflower	sea-island cotton, peanut
Drinks		coffee		tea	Korean ginseng		cacao	mate tea
Others	vegetables, fruits	melon, watermelon	hemp, garlic, onion, carrot, apricot, apple, pear, plum, almond, pistachio	vegetables, fruits		banana, sugarcane, fruits, spices	amaranthus, cotton, pepper	quinoa, amaranthus, tobacco, cotton, pepper
Established period (around)	8000 B.C.	2500 B.C.		4500 B.C.	4500 B.C.	8000 B.C.	5000 B.C.	
Farmland use	crop rotation, grass fallowing	continuous holticulture	nomadism in summer			shifting cultivation, bush fallow		
Seeding format	broadcasting	row sowing		roadcasting/mixed cropping, row sowing/intercropping, transplanting	transplanting	hill sowing, transplanting		
Farm implements	spade ard	hoe				digging stick		
Processing	kiln (powdered food)	polishing by vertical pestle		parboiling	*Shitogi* (wet milling), grain food	raw food, stoneware		
Food economy	abandance surplus, easy transportation	a little surplus	for self-sufficient			surplus, dificult transportation		
Establishment of a city state (around)	3000 B.C.			2500 B.C.	1600 B.C.		1000 B.C.	1500 B.C.

Murdock（1959）, Guyot（1964）, Nakao（1967）, Harlan（1979）, Sakamoto（1987）. Their hyposesises were modified.

The Indian subcontinent is diverse both linguistically and agriculturally. Within the context of the Renfrew/Bellwood hypothesis, the three major language groups of central and peninsular India have all been attributed to such language-farming dispersals, including Indo-European, Dravidian and Austro-Asiatic (the Munda sub-family). These hypotheses, however, have not been considered in detail in relation to either the archaeological, archaeobotanical or linguistic evidence relating directly to early agriculture in South Asia.

In southern India, archaeobotanical findings suggest the widespread presence of a core set of native staple crops throughout the Southern Deccan region. Notably, browntop millet (*Brachiaria ramosa*) and bristly foxtail (*Setaria verticillata*)—grasses found intermittently on wetter soils within the semi-arid Deccan savanna—were among these staples. Additional millets indigenous to peninsular India, such as little millet, *kodo* millet, *sawa* millet and yellow foxtail millet, have also been identified, although their status as cultivated crops is uncertain as they may have only been present in small quantities (Bellwood 2005; Fuller 1999, Fuller et al. 2001, Fuller 2002).

The proposed integrated model for the dispersal of Indian millets, as detailed in Figure 101, highlights several key stages. *Echinochloa furumentacea*, *Panicum sumatrense*, and *Paspalum scrobiculatum* emerged as secondary crops alongside upland rice. Initially, their ancestral forms were companion weeds originating from related species that had colonized paddy fields in the humid regions of Eastern India. These companion weeds evolved to become insurance crops within upland rice fields and subsequently spread into the drier areas of the Deccan Plateau (Kobayashi 1987, 1989).

Browntop millet (*Brachiaria ramosa*) and bristly foxtail (*Setaria pumila*) are considered tertiary crops, as they were secondary crops derived from other millet species that were themselves domesticated from related weeds in upland fields. In contrast, *Digitaria cruciata* has recently been traced to a related weed found in maize or vegetable fields in Kashi Hill, Meghalaya, and remains restricted to this locale (Singh and Arora 1972).

In summary, the domestication of Indian millet species likely occurred through a process of gradual diffusion, beginning with humid paddy fields in Eastern India and progressing to the dry upland rice fields of the Deccan Plateau in Southern India.

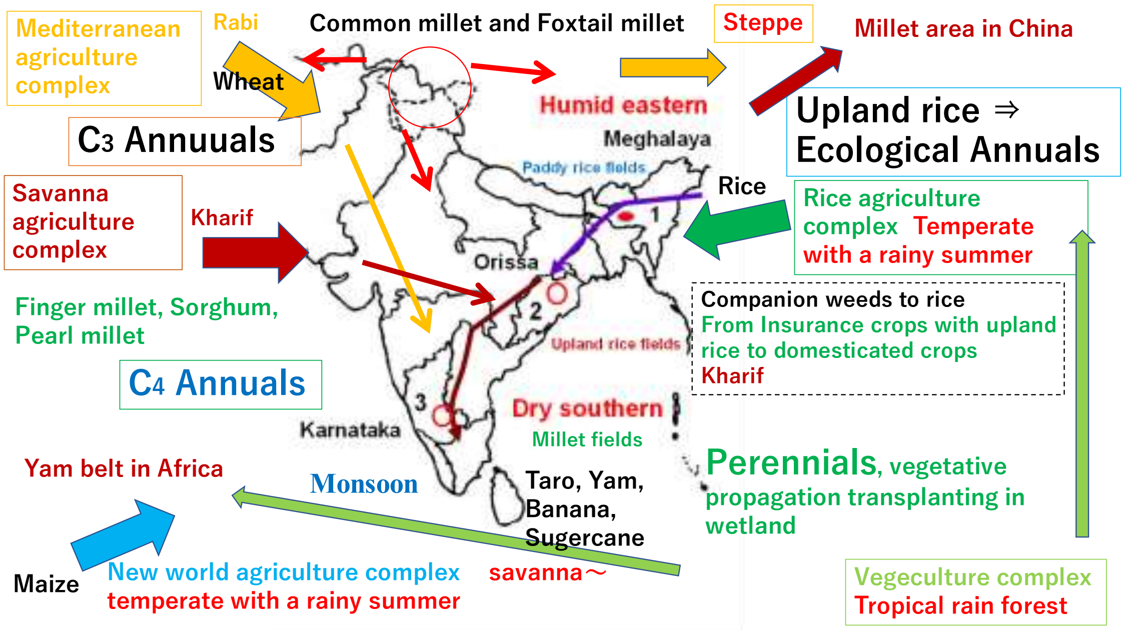


Figure 101. A new model of the domestication and dispersal of crops around the Indian subcontinent

Chapter 8. Biological diversity and Learning environment under the Anthropocene

Today, in the Anthropocene, humanity faces severe natural and artificial conditions, including climate change, natural disasters, and infectious diseases, along with the rapid advances in Information Technology and artificial intelligence (AI) and wars. These challenging circumstances are likely to lead to famine around the world.

Preserving Traditional Agricultural Practices in India

The traditional culture rooted in India's basic agricultural complex is hoped to remain unchanged for the future. Between 1983 and 2001, our field works on millet cultivation led to visit with over 100 farmers in rural villages across India. In the Deccan Platou of South India and hill and mountain regions of the East and West Ghats, farmers still rarely grow maize, as these areas are not fertile and receive little rain. *Mudde* prepared from maize flour is not popular; therefore, *upma*, *roti,* and *vada*, are prepared. In Pakistan, Nepal, and the millet-cultivation areas of Africa, maize has become a main grain produced in large quantities, and incorporated into traditional cooking styles (Kimata 1990).

This resistance to new trends may reflect the same spirit as Ganji’s spinning wheel, which preserved food traditions. During a first visit to India in 1983, many taxis in New Delhi were old and worn Ambassador cars and autorickshaws. Lord Krishna’s talisman could be seen pasted on broken speedometers, and it was not uncommon for doorknobs to come off or for headlights to be inoperable. In contrast, Pakistan and Nepal had many used Japanese Datsun cars on the roads.

Since 1968, the production of wheat, maize, and rice has increased through Green Evolution monoculture, while the millet production has declined. This shift has led to a reduction in the biodiversity of domesticated plants, resulting in the loss of numerous genes. Such a decline in diversity may hinder the ability of domesticated plants to adapt to the new regional/global environmental changes. Furthermore, The rich diverse culture of daily life, local foods, and traditional knowledge on nature faces the risk of being lost.

Form these observations, a clear difference emerges between farming and agriculture (Table 54). Farming is practiced as subsistence for families, with farmers growing daily foods and cultivating low volume of many varieties of crops. This approach fosters high biocultural diversity within local communities, and local farmers maintain high self-esteem. In contrast, agriculture is conducted as an industry, focused on state tax, strategic materials, and large-scale production of specific varieties of major crops. As a result, biocultural diversity is low and continues to decline (Shiva 1992, 1993).

Table 54. Comparing farming and agriculture

	Farming	Agriculture
Economy	subsistence, livelihood	industry, heavy investment of capital
Cultivation area	small scale	large scale
Worker	family	family, sharecropper, seasonal worker
Produce	daily food	taxes, commodities, strategic materials, biofuels
Crops	high-mix, low-volume production	mass production of specific crops
Cultivation method	organic	inorganic, use of pesticides and fertilizers
Biocultural diversity	high	standardization, low
Basic agricultural complex	inheritance of will	decline or none
Social form	local community	national government
Self-esteem, pride	autonomy, independence	other power heteronomy, progression of self-domestication

Large farmers and companies operate large-scale agriculture for generating money or trading (Table 55). Some major crops are adopted in the monoculture system for mass production, consumption, and discard. Biocultural diversity in plantation has decreased. On the contrary, a small-scale farming for family and local community has been practiced.

Table 55. Comparison between large-scale agriculture and small-scale farming

Large-scale agriculture	Small-scale farming
Plantation	Home garden
Large company for making money	Family to live
Industry/trade goods	Subsistence/self-sufficient food
Main crops/a few variety/monoculture	Diverse crops/many varieties/multiculture
Mass production/consumption/discard	Small quantity production/eat carefully/circulate
Decline of biocultural diversity/hard to sustain	Conservation of biocultural diversity/high sustainability

Compared with the lifestyle in Japanese rural villages, Indian farmers have cherished their traditional lifestyle (Table 56). However, as the population has rapidly increased in India following Green Evolution, large-scale agriculture became vital for mass production by the American agricultural systems. To address the social needs, some villagers and city dwellers promoted home garden, community gardens, and edible ways, in United Kingdom and Japan (Figure 102).

Moreover, organic farmers have their families involved with citizen-supported agriculture in suburban areas. Commercial interests are dominating, but subsistence remains very important.

Table 56. Comparison between rural village in India and rural village/suburbs in Japan

Rural villages in India	Rural village and suburbs in Japan
身土不二/one's birth are inseparable	身土分離/separation of body and soil
Circular farming/comply with the environment	Monoculture/not environmental friendly
Mostly Subsistence	Primary industry
Simple living	Convenient life
Sustainable rural society	Unsustainable urban society
Adaptable to the period in valley of wind 風の谷	**Against the revelation**
Deteriorating environment	Loss of traditional culture
Resource depletion	Massive import of resourcess
Population increase	Declining birthrate and aging population
	High suicide rate

Community gardens serve as vital facilities within urban environments, providing a place for resident to build relationships with their neighbors and foster sense of local community (Figure 102). Also, school gardens can improve nutrition and education for children and their families (Hunter et al. ed. 2020). School garden programs have been adopted as development interventions. In developing counties, these initiatives have focused on teaching enhanced farming skills, supporting community food production, raising funds, and demonstrating exemplary agricultural practices to communities surrounding the schools. Conversely, In industrialized nations, school gardens provide a broader educational function, helping children understand science, nature, and environmental processes. There is a growing recognition of the need to reconnect rapidly urbanizing school communities with the realities of rural life, local food culture, and biodiversity. The role of school gardens in environmental and nature education, local food biodiversity and conservation, food and eco-literacy, diets, nutrition and health, and agricultural education has been recognized. Over the last century, in Europe and the United States, school gardens have been featured as a hunger intervention. The Food Crops movement has grown, supporting school and community garden efforts. Learning about gardening, environmental processes, nature, and sustainable diets characterizes current school gardening efforts in Europe, Australia, and the United States (Gonsalves 2020, ed. by Hunter et al. 2020).

The Edible Schoolyard project, established in 1995 at a public middle school in Berkeley, California, exemplifies the global reach and impact of school garden programs. Nearly 25 years following its inception, the Edible Schoolyard has provided capacity-building support for teachers, administrators, nutritionists, food service staff, parents, and community leaders from more than 367 schools worldwide. Moreover, the project facilitates the Edible Schoolyard network, including 5,513 school garden programs globally. Under Edible Education, food is a tool to teach lessons of the academic curriculum (https://edibleschoolyard.org/). There are also other programs and practices, such as Crop Museums in Philippines, School Gardens in Australia, Burkina Faso and India, and Edible Schoolyards in Scotland and the United States.

The following two questions remain to be addressed: How exactly is the mental health and well-being of studies implicated in the practice of outdoor learning and gardening? How might we be able to design curricula that enhance and empower young people's ecological mindset and confidence? To answer these questions, collaborations with school counsellors, teachers, and students of all ages are vital to construct therapeutic garden spaces (School of Geographical and Earth Sciences, The University of Glasgow).

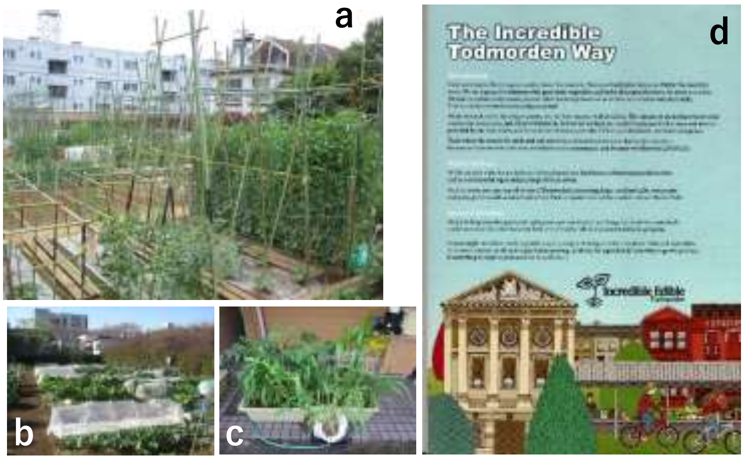


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Figure 102. Community garden and edible way

a・b, Community garden; c, edible way in Koganei, Tokyo; d, edible ways in Todmorden, UK.

The beginning of Anthropocene

The Anthropocene epoch began during the Quaternary period, marked by the Trinity test of nuclear weapons in 1945 and the subsequent bombings of Hiroshima and Nagasaki, Japan at the end of World War II (Table 57). The development and proliferation of nuclear technology continued with events such as the Chernobyl nuclear power plant accident in 1986 and the meltdown of the Fukushima Nuclear Power Plant following the Great East Japan Earthquake in 2011.

The term "Anthropocene" has become prevalent in scientific and social discourse, especially with respect to accelerating geophysical and biochemical changes. While it has not been formally adopted as a unit of Geologic Time Scale, the concept remains widely used by earth scientists, social scientists, politicians, economists, and the general public (Wikipedia 200225.10.29).

Following World War II, global consumption of fossil fuels significantly increased, driving continuous social changes in information technology/communication, the environmental change, and pandemic. Milestones including the Information Technology and Communication has developed very fast from the broadcast by television (1953), Internet popularization (1986), SNS popularization (2004), via Artificial Intelligence, to Chat GPT (2023).

Humanity faces the challenge of adapting the natural disasters, such as typhoons, earthquakes, and eruption, while also contending with artificial disasters, environmental pollutions, *Kogai*, famines, wildfires of forests, microplastics, organic fluorine compounds, and microplastic. The global population has surpassed 8.3 billion as of October 29, 2025. Population growth, couple with the increasing the number of livestock, has contributed to the emergence of various infectious diseases, including influenza, coronavirus, bird flu, and swine fever. Since the Green Revolution, scientific and technological advancements have led to genetic modification, completion of the human genome, and genome editing.

Anthropocene may be the chaotic Kali Yuga of Hinduism, yet there remains hope for the future.

Table 57. Social changes over Anthropocene

A.D.	UN Declaration and International treaty	Nuclear power	Information and Communication	Environmental change	
				Artificial disasters	Natural disasters
1943				Bengal famine	
1945		Trinity test, Atomic bomb dropped on Hiroshima and Nagasaki		World War II, and then incleased usage of fossil fuel	Makurazaki typhoon
1948	Universal Declaration of Human Rights			Expansion of Afforestation	Earthquakes in Fukui and Turkmenistan
1953			Start of broadcast by TV	Increase rapidly the emission of CO_2, in 50'^{s}	
1954		Bikini Atoll hydorogen bomb test, Radiation exposure of Daigo Fukuryu Maru		Inclease in new chemicals	Climate change
1956				Minamata disease, Yokkaichi asthma （～1970'^{s}）	
1959				Itai-itai disease （1910～1970'^{s}），The Great Chinese Famine	Isewan typhoon
1963		Power generation of Power test reactor/JPDR		Pollinosis （1961）	
1968				Green Revolution	
1970	Treaty on the Non-Proliferation of Neclear Weapons				Cyclone to Bangladesh
1972	Human Environment Declaration	Termination of Vietnam War			
1976					China/Tangshan earthquake
1979		Three Mile Island Nuclear Power Plant accident		Genetic modification （1980'^{s}）	
1986		Chernobyl Nuclear Power Plant accident	Internet popularization		
1993	Convention on Biological Diversity			Sick building syndrome （1990'^{s}）	
1995					Great Hanshin-Awaji Earthquake
1999					Orissa super cyrlone
2001					Gujarat Earthquake
2003				Completed Human Genome	
2004			SNS popularization		Indian Ocean earthquake and tumami
2005				Genome editing	
2006				Peak oil	
2007	Declaration on the Rights of Indigenous Peoples				
2008					Cyclone to Myanmar
2009					
2010	UN Decade on Biodiversity				Haiti Earthquake
2011		Meltdown at Fukushima Nuclear Power Plant		Spread of radioactive materials	Great East Japan Earthquake, Tsunami
2014					Eruption of Mt. Ontake
2015					Typhoon 18 heavy rain
2016	UN Decade of Action on Nutrition				
2017	Treaty on the Prohibition on Nuuclear Weapons			CRISPR system	
2018	Declaration on the Rights of Peasants				
2019	UN Decade of Family Farming				
2020			Artificial Intelligence AI, Big data analysis		
2021	UN Decade of Biodiversity				
2022		War of aggression to Ukraine by Russia			
2023	International Year of Millets	Marine drainage of contaminated treated water at Fukusgima	ChatGPT	Organic fluorine compounds, micro plastic	Moorocco Earthquake, Libya flood, Forest fire
2024		Israel Invasion on Gaza			Noto Peninsula Earthquake
2025				Wildfire	

Domestication of plants, animals, and the self-domestication of humanity

To understand the domestication of plants and animals, as well as humanity's own self-domestication, it is essential to first clarify the concept of "domestication." This concept has been explored through various case studies discussed in previous chapters. Table 58 provides a clear definition regarding the domestication of plants and animals, as well as the self-domestication of humanity.

In the Tertiary period, the biological evolution of wild species governed solely by natural selection. With the advent of Anthropogenesis during the Pleistocene, Quaternary, the artificial selection by human had added to the harsh natural selection. Cultural evolution then progressed under the unsparing Nature. Under strong artificial selection pressure, humans and domesticated plants co-existed via their symbiotic evolution. However, the plants can escape somewhat human influence by hybridizing naturally with wild spices or weed. Weeds and crop have a close relationship, especially in the tropics where weedy and cultivated varieties have genetically interacted and hybridize freely to produce new varieties.

Self-domestication in humans is defined by the profound effects of artificial selection operating within urban societies, where many have lost connection with nature lost touch with nature. This process can lead to various forms of degeneration as living being, including reliance on artificial feeding, substitution of artificial intelligence for independent thought, and a preference for convenience achieved through excessive use of energy and machinery. Adapting to the Anthropocene, the subordinate evolution was prompted under the hyper-domestication process. Investigators have initiated artificial genetic changes and had produced unnatural foods.

Table 58. Definition of the domestication of plants and animals, and self-domestication of humanity

Geographical period	Era and evolutionary style	Characteristics
Tertiary	biological evolution	wild species under natural selection
Quaternary/Pleistocene	2,580,000 years ago	Anthropogenesis
Semi-domestication process	cultural evolution	under harsh natural selection in addition to human artificial selection
Quaternary/Holocene	11,700 years ago	
Domestication process	symbiotic evolution	by the strong artificial selection pressure on domesticated plants, and human preservation, the natural selection had become inapparent. However, the plants had been able to escape from human action.
Quaternary/Anthropocene	from 1945	
Hyper-domestication process	subordinate evolution	Investigators have initiated the artificial genetic changes and then they had produced unnatural foods.
Self-domestication by human itself	regressive evolution	Very severe artificial selection has the profound effects among each human lived in urban societies where have lost touch with nature. Degeneration as a living thing: feeding, substitution of AI for self-thinking, convenience by overuse of energy and machinery.

Currently, the self-domestication of humanity in the Anthropocene is a particularly significant issue. Several properties of this process are outlines in are listed in Table 59. The concept "self-domestication" is defined as the process in which humanity as both the creator and torchbearer of culture, shapes itself within its own cultural environment. Unlike the domestication of animals and plants by humans, self-domestication in humans occurs by their own actions and choices, not by another species.

The definitions and perspectives provided in Tables 58 and 59 are drawn from numerous authors, including Yamamoto et al. (2009), Obara (1995), Parson (2020), Kumashiro (2024), and Harari (2015).

Relationship between the genesis of city-state, polis, and grains

The emergence of polis is closely associated with the domestication of cereals, as these grains became the basis for taxation and state power over thousands of years. Scott (2009, 2017) proposed a novel hypothesis on the origin of states, focusing on the region known as Zomia, which stretches from the Central Plateau of Vietnam to Northeast India. This area is notable for its ecological diversity and the presence of many ethnic minorities, some of whom have intentionally remained outside the jurisdiction of any state.

Traditionally, Sedentism and the rise of towns are viewed as outcomes of irrigation and state formation. However, settled living and civilization led directly state formation long after fixed-field agriculture appeared. Cereal grains uniquely served as a basis for taxation because they are visible, divisible, assessable, storable, transportable, and “rationable.” While other crops – legumes, tubers, and starch plants– have some of these desirable state, adapted qualities, none has all these advantages.

Grain hypothesis: Virtually all classical states were based on grains, including wheats, millets and rice. History records no cassava, sago, yam, taro, plantain, breadfruit, or sweet potato states. State formation becomes possible only with few alternatives to a diet dominated by the domesticated grains. In Neolithic villages, which often arose in water-rich areas, subsistence was based on hunting and foraging with some evidence, though debated, of cereal horticulture and livestock rearing. The first large, permanent settlements developed in wetlands, relying on wetland resources, rather than grains, negating the need for irrigation in the conventional sense (Opie and Atkinson 2025).

Population concentration in these areas did not lead to state formation unless large-scale grain cultivation was present. The unique properties of cereal grains made them ideal from the perspective of ancient tax collectors, who prioritized ease and efficiency of appropriation. In contrast, shifting or slash-and-burn cultivation depended on the biodiversity of traditional root vegetables and tubers, making taxation difficult and thus disfavored by states. Consequently, mountain people practicing such agriculture were often labeled as “savage,” while flatland rice growers were seen as “civilized.” Infectious diseases were less common in mountainous regions, partly due to lower mosquito populations. The people of these regions relied on “rescue foods” such as taro, yam, sago palm, and more recently, cassava, maize, and sweet potato, allowing them to maintain a degree of independence from state control.

Humans tend to view themselves as the central agents in stories of domestication (Table 59). We domesticated wheat, rice, sheep, pigs, and goats. However, from a different perspective, it could be argued that we are actually the ones who have been domesticated

Table 59. Several properties on the self-domestication of humanity

Self-domestication	Definition	*Homo sapiens* are creator and also torchbearer of culture. They put in their cultural environment. On the case of human self-domestication, they had not been domesticated by the other species, but they had been done by themselves.
Evolution of friendliness	Optimism	*Homo sapience* had acquired the friendliness toward same as well as diffferent species by natural selection; thus they could prosper, even when ohers got extinct.
Dietary life of hunter-gatherers	A case of integrated mind; Think experientially by oneself	A case study on Hadza in Tanzania: Everyday people go outside lookiing for food, return to their campsite, and cook/eat/sleep with their family. The ape dose not take food home.
Dietary life of city people	A case of self-domesticated mind; depended on the external information device	City-dwellers purchase microwaved foods at the spermarket; they cook food unusually. They usually eat meal alone at dining rooms or cafeteria.
Prejudice	discrimination	negative emotions against a population.
Evil forces	A pessimistic view, genocide	When humans feel threatened, they can ignored different groups; the norms of humane treatment are no appilicable.
Self-domestication syndrome of animals	distinguish between human and animals	Domesticated annimals become obedient as a result of genetic adaptation. The process of reactive aggression is called 'a self-domestication'. Human is the creator as well as torchbearer of culture. They create their cultural environnment. Humans had not been domesticated by other species, but had self-domesticated.

Hare & Woods (2020), Kimata (2012), Mithen 1996, Omoto ed. (2002), Wranganer (2019) cited.

Millet production during wars and disasters (2019)

Shiva (1991) highlighted the regressive evolution linked to the concept of self-domestication, emphasizing that the main threat to living with diversity arises from “Monocultures of the Mind.” This mindset erases diversity from perception and reality, leading to the disappearance of alternatives and the rise of TINA (there is no alternative) syndrome. In contemporary society, the total uprooting of nature, technology, communities, and entire civilization is justified on the grounds that ‘there is no alternative.’ Although excluded, alternatives exit and their inclusion requires a context of diversity. Creating space for these alternatives requires a fundamental shift toward diversity in thought and action, which allows for multiple choices to emerge.

Protecting native seeds is not solely about conserving raw material for biotechnology; it is also about preserving ways of thinking about nature and alternative modes of production. Native seeds serve as a form of resistance against monocultures and monopoly right. Embracing diversity as both a way of thought and a way of life is crucial to countering the impoverishment brought by monocultures of the mind.

Dominant systems render local knowledge invisible by declaring it non-existent or illegitimate. They also erase alternatives by destroying the realities these alternatives seek to represent. The fragmented, linear nature of dominant scientific knowledge disrupts the integrations between systems, fostering a monoculture of the mind and undermining local alternatives, much like the displacement of local plant diversity by introduced monocultures.

Crops are often labeled as marginal or coarse grains are some of nature’s most productive crops in terms of nutrition. Women in Garhwal continue to cultivate *mandua* (finger millet) and those in Karnataka cultivate *ragi* (finger millet) in spite of all attempts by state policy to shift to cash crops and commercial foodgrains, to which all financial incentives of agricultural development are tied.

One woman in a Himalaya village once indicated to be that ‘Without our *mandua* and *jhangora* (Indian barnyard millet), we could not labor as we do. These grains are our source of health and strength.’

The value of farmers’ and tribal seeds is high in social and ecological terms, even if the market system fails to recognize it. The limited ability of the market system in assigning values can hardly explain denying values to farmers’ and nature’s seeds (World Rainforest Movement 1991).

The reduction in the availability of fertile land and genetic diversity of crops due to Green Revolution practices indicates that at the ecological level, the Green Revolution produced scarcity, not abundance. Green Revolution refers to the science-based transformation of Third World agriculture. The Indian Panjab was its most celebrated success. Paradoxically, after two decades of the Green Revolution, Punjab is neither a land of prosperity or peace.

The millets, minor cereals occupied the largest area under cultivation in Punjab, are diverse, not because they are insignificant crops. *Kutki* (*Panicum miliare*, syn. *P. aumatrense*), *jawar* (*Sorghum vulgare*, syn. *S. bicolor*), *mandal* or *chalodra* (*Eleusine coracana*) and *bajra* or bulrush millet (*Pennisetum typhoidenam*, syn. *P. americanum*) were the primary millets cultivated in Punjab, covering 43% of the area. Besides, there are also uncultivated or wild varieties of millet, such as *shama* (*Panicum hydaspicum*), *Cenchrus echinatus*, *Pennisetum cenchroides*. In addition to these, the more well-known cereals were *makki* or maize and wheat.

As a result of the Green Evolution in Panjab, common lands under forests and pastures have been placed under agricultural crops. As the Green Revolution spread, local community management broke down and grazing lands and forests were broken up for monoculture cultivation.

Swaminathan (2022) identified two major paradoxes of global food systems: the persistence of hunger despite technological advances in food production, and the narrowing crops diversity within global food systems in the face of a fast-grow world population. The yields of major crops are plateauing, and overcoming this challenge will require innovative solutions. Agro-biodiversity should be leveraged to produce more and diverse nutritional foods in areas with poor soil and challenging climatic conditions. This is not a new concept since risk-aversion practices have guided generations of farmers who have been growing different crops and varietal mixes to buffer against shocks. Farming families have often been motivated by a desire to minimize risk, not just maximize profits; hence, the wisdom behind the decisions to balance subsistence and market motivations needs to be recovered.

Case study: Millet cultivation in wartime Japan

The cultivation area of millets increased in wartimes Japan. The Japanese government promoted millets cultivation through numerous booklets aimed at combating hunger. The booklets were printed on the day before dropping the first atomic bomb on Hiroshima, and then Nagasaki. Anthropocene was initiated after Hiroshima followed on Trinity Nuclear Test.

The millet production of modern Japan is shown in Table 60 and Figure 103. The total production was approximately 350,000 ha (cho 町≒ha) in 1900’s. Subsequently, production gradually declined outside of wartime conditions, and by 2023, millet cultivation had become nearly extinct.

Table 60. Millet production in Japan

Millet	1900	1950	1990	2001	2002	2003	2023
Foxtail millet	243,700	66,100	44	50	53	44	
Common millet	34,100	26,200	146	169	152	121	
Japanese barnyard millet	71,900	33,200	290	110	150	156	
Sorghum	The Russo-Japanese war (1904)					22	
Job' tear				344	312	358	
Finger millet	World War I (1914~1918)/II (1939~1945)					trace	
Total	349,700	125,500	480	673	667	701	251
Buckwheat				41,800	41,400	43,500	35,500
Tartary buckwheat						14	
Amaranth				15	11	18	

農産業振興奨励会2001～2003、**新需要穀類等生産・流通体制確立事業実績報告書**

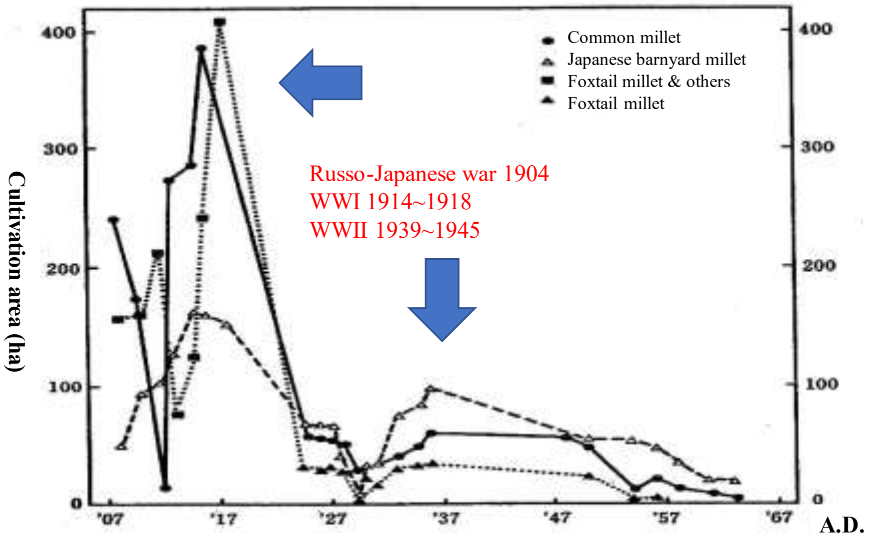

Figure 103. World War I/II and cultivation area of millets in Japan.
Books on Japanese barnyard millets and traditional foods in war time.

For instance, one farmer prepared food grains of foxtail millet and upland rice in the storehouse for famine (Figure 104). Another old farmer continues to cultivate numerous local millet varieties for seed conservation. These villages were well-known for the exceptional longevity and health of their resident. Exemplary farmers in the region maintain indigenous millet varieties and upheld advanced farming methods. Numerous researchers have visited these villages in this area of Kanto mountains, Central Japan. We have held the exhibitions of millet cultural complex in many places.

Figure104. Storehouse at a farm for food security in Fujino, Kanagawa, Japan
a, Storehouse; b, inside; c・d, local variety of foxtail millet; e, local variety of non-waxy upland rice; f, waxy rice variety.

The Great East Japan Earthquake struck northeastern Japan on March 11, 2011 (Figure 105a, b). Most of the paddy fields had washed away by the repeating waves of big *tsunami* in the coastal area. However, the upland field had not washed away, since the waves did not reach the hill regions. Consequently, local famers had reaped their harvest of millets and other crops (Figure 105c, d).

Figure 105. Landscapes of seaside and hillside after Great East Japan Earthquake
a, Paddy fields washed away; b, overgrowth of weeds; c, no damage of millet field on hillside; d, the harvest.

Conservation of the biological diversity of our seeds and foods

Despite recent trends, we have preserved many local varieties of millets and traditional crops for decades. We showcased our projects by Working Group for People and Seeds for the Future, Japan Civic Network for CBD at the Conference of the Parties; CBD/COP10, Nagoya 2010 (Figure 106).

Conference of the Parties; CBD/COP10
Nagoya 2010
Japan Civic Network for CBD
Working Group for People and Seeds
for the Future: exhibition booth/
Booklet/Position paper

Figure 106. Conference of the Parties; CBD/COP10, Nagoya 2010

Local varieties of crop seeds have the social common capital, belonging to local farmers and communities. After the Great East Japan Earthquake on March 11, 2011, I had transferred our millet accessions (c.a. 10,000 accessions of seed samples) to Millennium Seed Bank, Royal Botanic Gardens Kew (Figure 107), since we had to prevent them from the scheduled blackout and radioactive rays (expedited on June 22, 2011).

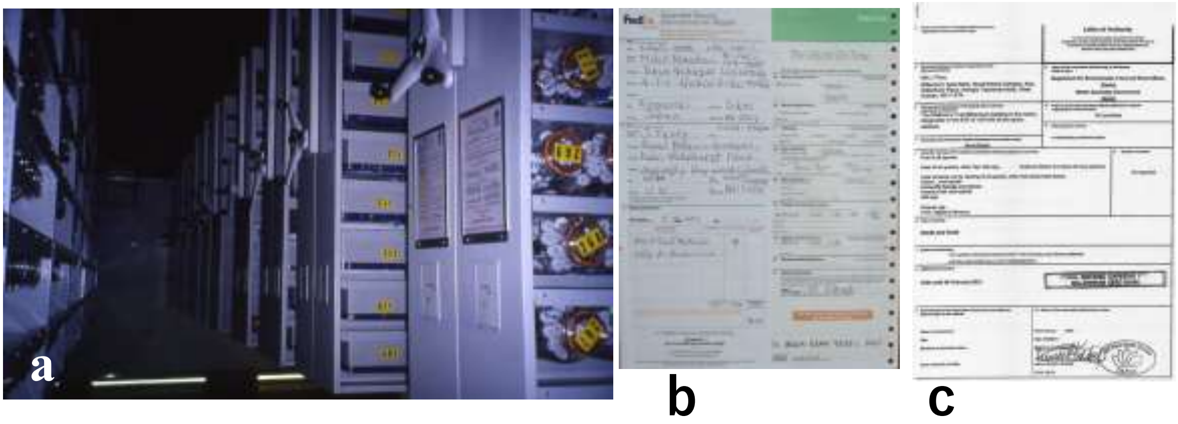

Figure 107. Millenium Seed Bank of Ryal Botanic Garden

a, Storage room; b, FedEx cover letter on June 22, 2011; c, acceptance certificate.

Throughout the 20th century, societies worldwide have faced numerous social phenomena, including droughts, wars, and famines (Table 61). For example, India experienced three major episodes of widespread hunger: the devastating drought of 1900 with an estimated 3,250,000 deaths, the Bengal famine of 1943 with up to 3,500,000 deaths, and the drought of 1965 resulting in around 1,500,000 deaths. These events highlight the critical importance of food security and the preservation of resilient crop varieties.

The total global population exceeds eight billion, and global grain production is approximately 3.9 billion tones. Millets and others were cultivated in 137 nations in 2021. The percentage of production were 9.7%. Millets and others were consumed by over 0.7 billion people in Afro-Eurasia. The population of Japan represented 1.6% of the world’s population, while the grain production was only 0.3% in 2021. Japan must produce more grains for food security. We distributed millet seeds to citizens for farming.

Table 61. Drought, war, and famine in the 20th century

Common Era	Area	Cause	Number of starvation-related deaths
1900	India	drought	250,000~3,250,000
1918	Germany	World War I, bad harvest, Turnips in Winter (1916~1917)	762,000
1918	World	war dead	8,529,000
1921	Russia	drought	5,000,000
1928	North China	drought	3,000,000
1932	Ukraine	Holodomor, policy of USSR	2,600,000~10,000,000
1932	Kazakhstan	interlocking Holodomor	1,200,000~1,500,000
1936	China	drought	5,000,000
1941	Russia	besiegement by German army	1,000,000
1941	Greek	occupation by German army	300,000
1942	China	Henan famine, invasion by Japanese army	2,000,000~3,000,000
1943	India	Bengal famine	1,500,000~3,500,000
1944	Netherlands	World War Ⅱ, Famine winter	22,000
1944	USSR	Siege of Leningrad	1,000,000~1,500,000
1945	World	World War Ⅱ	20,000,000
1945	World	war dead	19,500,000
1947	USSR	bad harvest, restrictions on annexed land	1,000,000~1,500,000
1947	China	Great Leap Forward policy	36,000,000
1965	India	drought	1,500,000
1968	Sahel	drought	1,000,000
1975	Cambodia	policy of Khmer Rouge	2,000,000
1996	North Korea	flood damage, Arduous March	220,000~3,500,000
1998	Congo	civil war	3,800,000
2020~2021	World	Coronavirus deaths	15,900,000
	Japan		
1732	Kyoho	bad harvest, locust invasion	1,000,000
1782	Tenmei	bad harvest	1,100,000
1833	Tenpo	bad harvest	300,000
1930	North-East	bad harvest	not clear
1945	domestic and overseas	World War Ⅱ, invasion by Japanese army	850,000~1,400,000
1945	Japan	war dead (including the above)	3,100,000
1946	domestic	bad harvest, after the defeat in war	not clear
1993	North-East	bad harvest	0
2011	North-East	Great East Japan Earthquake	22,228

Following the Green Evolution, the grain production concentrated on three major cereals: high yield varieties of wheat, maze and rice. The cultivation area of other cereals significantly decreased; however, we can recognize the production of the other cereals, such as, rye, oat, sorghum, millet, and buckwheat for our subsistence in the war time of Ukraine. On the contrary, Japan keeps only rice production, but the other cereals are cultivated only trace (Table 62). Majority of Japanese inhabit in urban area, which does not involve their subsistence, and buy imported foods. The hunger of wartimes or disasters became distant history.

The productions of millets and sorghum have increased in many nations (Table 63) (FAOSTAT 2022). Millets are nutritious grains that grow under the harsh environment. FAO had held the International Year of Millets in 2023 to re-evaluation those orphan crops. Especially in India and African nations, the production of millets and sorghum are increasing. It is important that the production of sorghum is increasing in USA, Mexico and Brazil.

Common millet is continued to grow in many places throughout Eurasia (Figure 108). We have purchased some in European countries' markets.

Table 62. Comparison of crop production between Ukraine and Japan.

Cereals	**Ukraine**		**Japan**	
	Nation area ㎢	**Population**	**Nation area ㎢**	**Population**
	604,000	43,734,000	378,000	126,47,6000
	Cultivation area ／ha	**Production ／tone**	**Cultivation area ／ha**	**Production ／tone**
Winter				
Wheat	6,564,500	249,123,500	212,600	949,300
Barley	2,374,500	7,636,340	63,600	221,700
Rye	137,800	456,780		
Ort	199,000	510,000	165	317
Summer				
Maize	5,392,100	30,290,340	62	164
Rice	11,200	60,680	1,462,000	9,706,250
Sorghum	47,200	106,560		
Millet	159,100	256,050	295	247
Buckwhwat	84,100	97,640	66,600	44,800
Soy bean	1,364,300	2,797,670	141,700	218,900
Sunflower	6,480,900	13,110,430		

FAOSTAT(2020)

* Common millet in Ukuline

** Japanese barnyard millet, foxtail millet, common millet

Table 63. Production of millets and sorghum (FAOSTAT 2022)

Nation	**Millets**		**Nation**	**Sorghum**	
	Area/ha	**Production/tone**		**Area/ha**	**Production/tone**
India	8488150	11849190	**Sudan**	7000000	5248000
Niger	6780623	3656958	**Nigeria**	5700000	6806370
Sudan	2500000	1675000	**India**	3800810	4150570
Mali	2104437	1844664	**Niger**	3786257	2100697
Nigeria	2000000	1941220	**Burkina Faso**	1958672	2013869
Chad	1194064	694196	**USA**	1849430	4769960
Burkina Faso	1043257	907745	**Ethiopia**	1660000	4200000
Senegal	969693	1097033	**Mali**	1639394	1603394
China	900310	2700495	**Mexico**	1332929	4754169
Ethiopia	455000	1150000	**Brazil**	1043480	2923318
Japan	285	251	**Japan**	0/trace	0/trace

Figure 108. Sale of millets in European supermarkets

A structure of the environment learning process for life, for creating the fundamental theory of environment learning

The primary purpose of environmental education in Japan is to deliver information on global issues. Most specialists do not reach a basic agreement on the systematic methodology of environmental education study. It is the fundamental theory of environment learning that everyone must learn the environment around them, to develop aptitude and individual nature and live comfortably. The methodology of environmental education has remained mostly at the practical stage, and has not advanced beyond the theoretical stage.

Today, modern humans no longer interact directly with the natural environment. Instead, they have significantly advanced cultural evolution and developed complex civilizations through scientific and technological capabilities. The capacities that made up the “mind structure” of human beings have lost their integrating function as a result of urbanization and the development of computer programming languages. It is a fundamental environmental issue that urban residents cannot learn from or understand the environment as they do in rural areas. Modern people need to acquire scientific knowledge in schools and experience traditional knowledge in rural communities. They must learn the environment for recovering the integrating function and nurture their worldview to foster fertile lives throughout their lifetimes.

I propose a working hypothesis, named “a Structure of the Environment Learning Process for Life,” illustrated in Figure 109. This model integrates all knowledge of subsistence, science, their relationship, and intuition into an individual’s “mind structure.” It is desired to promote theoretical studies grounded in educational practices to designate a new subject, “environmental studies,” in school education as a result of the research meeting on the environmental studies curriculum. Moreover, it is necessary to construct “the Fundamental Theory of Environment Learning.”

Environmental education studies is an integrated domain encompassing numerous sub-domains, such as ecology, geography, anthropology, environmental sciences, and pedagogy. An integrating framework is needed for environmental education programs to practice and research. The Kaleidoscope system has been proposed as a kind of framework for environmental education programs (teaching/learning), as illustrated in Figure 109 (Kimata 1990). The system consists of 10 programs: (1) basic programs: N, natural history; C, cultural history and W, world view; (2) relating programs: M, making; T, thinking and feeling; (3) integrating program: P, play; (4) action programs: L, local, Co, cooperation and Con, conservation. We hope to reach the goal (six objects) of environmental education effectively through the system. The cooperation program is one of the action programs in the Kaleidoscope system. This cooperation program closely aligns with the partnership networks that promote environmental education for a sustainable society.

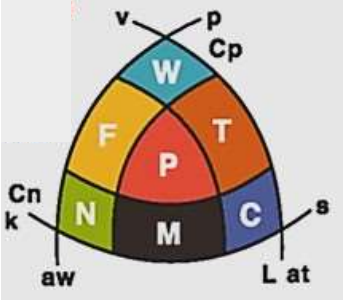

Figure 109. Environment Learning Framework (ELF)

N, nature; C, culture; W, world view: F, feeling; M, making; T, thinking; P, playing. Cn, conservation; Cp, cooperation; L, local. aw, awareness; k, knowledge; s, skill; at, attitude; p, participation; v, value.

Learning environment framework based on ethnobotanical aspect

Throughout Anthropocene, *Homo sapiens* have diverged from their natural origins. Today, the majority of people reside in urban environments, with most working in offices, lacking firsthand subsistence experiences such as gathering, hunting, fishing, or farming. Consequently, they have failed to develop wholesomely the structure and function of their minds under historical situations.

The human mind is composed of five intelligences (Figure 110): natural history, technical, social, general, and linguistic. Its function consists of seven senses (Figure 111): eyesight, hearing, taste, smell, touch, intuition, and conscience. These five intelligences and seven senses are developed in a learning environment. We propose a model for the learning process in this environment. In the 10 learning programs, an integration program Play is the beginning of learn.

Human cultural evolution rapidly developed during the Holocene, Quaternary period, driven by the domestication of plants and animals, and the use of fire, tools, and language. These phenomena depended on the cultural evolution of the human mind, which led to their civilization. Today, convenient cities are being created in surplus. Urban residents are fed artificial foods, and their thought are dependent on AI through big information technology.

This indicates that self-domestication of *Homo sapiens* has evolved. Humans do not grow grains or vegetables, but purchase them. In addition, we use convenient tools, such as smartphones and personal computers, and do not think much about nature, subsistence, and social living. We must learn about the environment deeply to prevent excessive self-domestication and rehabilitate and develop our minds through diverse experiences in nature and rural areas toward the civilization of living things.

Mithen (1996) explored the evolution of the human mind throughout history, noting the emergence of distinguishing features, such as language and an advanced intelligence. Understanding these developments provides insight into what it means to be human. The onset of farming is frequently invoked as the turning point of prehistory. Without agriculture, towns, cities and state society would not have existed. The rise of agriculture was a direct consequence of the type of thinking evolved with cognitive fluidity. More specifically, there were four aspects of the changes in the nature of the human mind that led to a reliance on domesticated plants and animals during abrupt environmental changes approximately 10,000 years ago:

Moreover, Mithen explained the origin of agriculture and four aspects of change in the nature of mind. 1) The ability to develop tools to harvest and process plant resources. This arose from an integration of technical and natural history intelligence. 2) The use of animals and plants as the medium for acquiring social prestige and power. This arose from an integration of social and natural history intelligence. 3) The formation of social relationships with plants and animals, structurally similar to those developed with people. This is a consequence of an integration of social and natural history intelligence. 4) Manipulation of plants and animals, arising from the integration of technical and natural history intelligence. When people were faced with the cognitively fluid mind that enabled them to find a solution, agricultural lifestyle was developed. Nevertheless, agriculture fundamentally changed the developmental contexts for young minds: for most people alive today, the world of hunting and gathering, with its specialized cognitive domains of technical and natural history intelligence, became no more than prehistory.

I have modified Mithen' s theory (1996) in Figure 110. Holistic humanity once possessed integrated intelligences, but this unity was disrupted during self-domestication in modern civilization. As language evolved, it was transformed into information and, eventually, artificial intelligence. Despite advancements in civilization and technology, the importance of natural intelligences—including general intelligence—remains essential for the future.

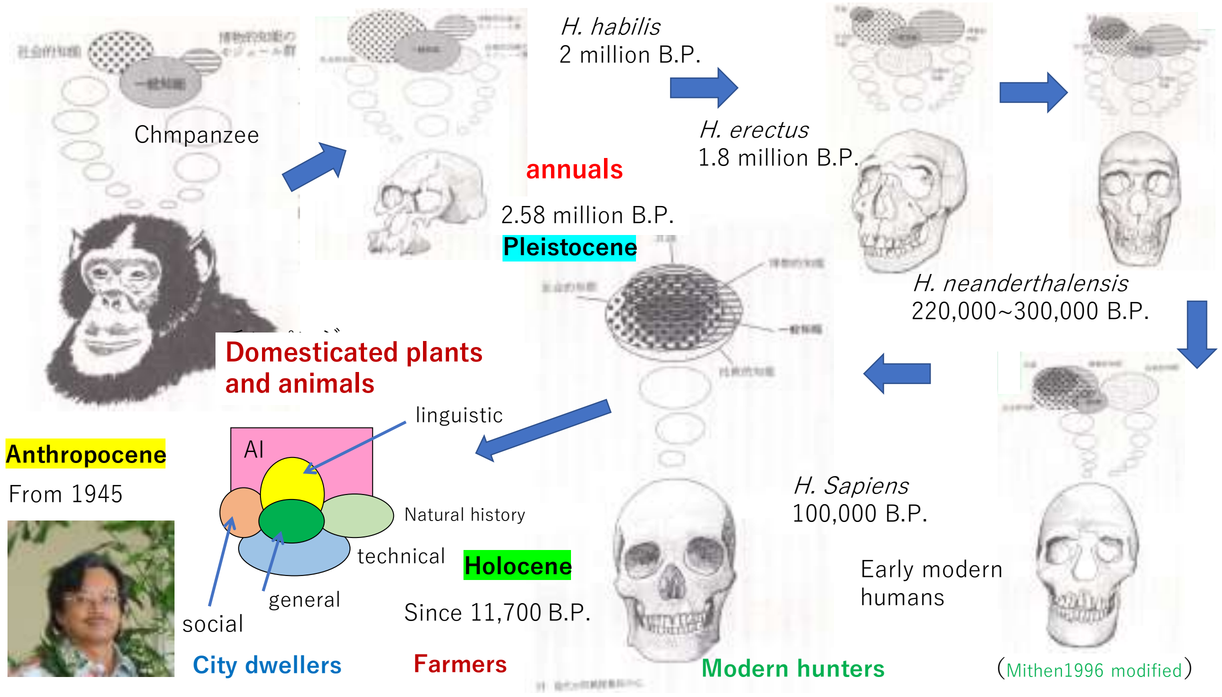

Figure 110. Evolution of the human mind during Quaternary transition

This framework had been inspired by “The Evolution of Mind in Prehistory” (Mithen 1996), "Human, Play and Nature," (Iwata 1986) and "the sociopath next door" (Stout 2005).

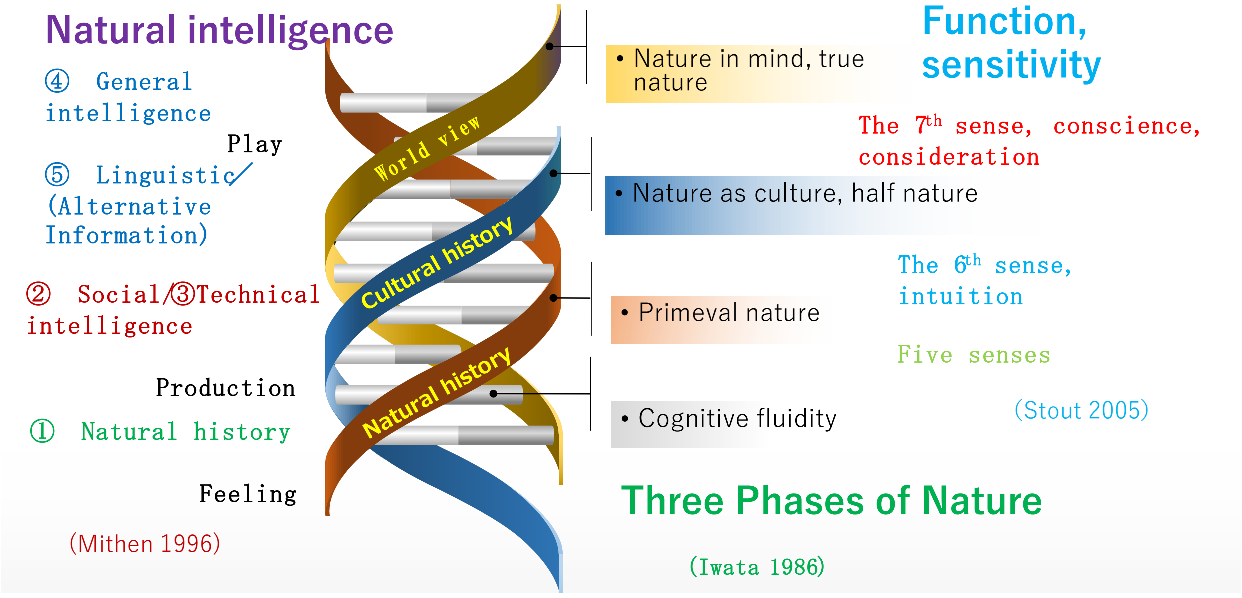

Figure 111. Auxiliary work model for the structure, function, and cognitive fluidity

Case studies in Japan and other regions

People exhibit strong interest in global and local environmental issues, such as the greenhouse effect, acid rain, deforestation, desertification, biodiversity erosion, and population explosion. Locally, concerns extend to drainage, garbage disposal, noise, food contamination and security, and radioactive contamination. Therefore, environmental education is vital, as it plays an important role in solving those problems. Its principal aim is to support the personal learning to hand on or re-create traditional knowledge appropriate to local natural conditions. Through environmental studies, people acquire integrated knowledge and skills to conserve natural and cultural heritage while maintaining comfort of their lives. Environmental education is an essential part of lifelong education.

The root cause of environmental problems is often a lack of environmental learning. The goal of environmental education/learning is to inherit nature and culture and create a sustainable society. Environmental education studies are based on environmental studies, a newly integrated domain from a holistic viewpoint. This domain is not in natural and social sciences as an analytical domain. The six objects of environmental education have been well discussed (Belgrade Charter 1975). Environmental education/learning include outdoor activities of nature observation and camping, separating activity of garbage and form values based on the learning scientific and traditional knowledge and the activities of environmental conservation and creation. Therefore, a holistic structure of the environmental education/learning and should be presented to position each program in the structure. Kimata (1990) proposed Environment Learning Framework (ELF) as a framework of environmental education/learning, educational methodology and practice for creating the sustainable society (Table 109).

I. Philosophy on Environmental Education Studies and Teaching/Leaning Activities for Environmental Education ELF: N, C, W

1) What is environmental education? Searching an environmental education for sustainable society.
2) The three phases of nature and a framework of environmental education program
3) Short history of environmental education in Japan
4) A model of curriculum for environmental education
5) Teaching/learning activities for environmental education

II. Partnership Network and Policy for Environmental Education ELF: C, Co, L
Networks, partnership and linkages for sustainable society
Environmental education partnership network in the Asian-Pacific Region
Environmental education partnership network in Japan
Environmental education partnership network of Tokyo Gakugei University
A workshop for ODA in education

III. Ethnobotany of Traditional Agriculture and Rural Communities ELF: Cn, Co, C, N, M, L
Introduction
Means of rural communities as an environmental culture: millets, traditional knowledge and environmental conservation
A case study 1: coevolution of Indian millets between human beings and plants
A case study 2: NPO-Native Seeds/SEARCH in USA
Some issues in urban and rural communities
Exchange program through environmental education among people lived in city and village

IV. GLOBE Program Activities in Japan ELF: N, Cn, Co
Beginning and today
Goals of GLOBE Program

V. Millet Straß Promotion Association ELF: N, C, M, Cn, Co
Seminar
Cultivation training

Application cases

1) Formation of vernacular names for weeds and plant naming programs to re-create children's culture ELF: N, C, T

Research on vernacular names was conducted for weed species in the genus *Rorippa*, Cruciferae, comparing linguistic modes and meaning among scientific, English, and Japanese standard and vernacular names. Standard names were mainly derived from morphological and ecological traits and place-names, while vernacular names were uniquely formed by local farmers. The result of that study provided crucial insight for the plant naming program (Kimata et al. 2007).

The plant naming program was applied twice to the activities of Dokodemo Museum Eco-Project and Nukui Agriculture School for Boys and Girls in 2004. The study primarily involved primary school children. The children were required to name a plant after observing them and their habitats in the fields. The names given by the children had the structure of {adjective word + root +

supplementary word} or consisted of unique words without any root. The root was mostly a word indicating a plant habit or organs, such as herbs, flowers, seeds, and leaves. The adjective word often showed morphological, ecological, and sensuous traits or their composition. The supplementary word was rarely used when the children hesitated to name a plant. At the same time, they drew sketches of plants and searched for further information in illustrated plant dictionaries. After reviewing the Japanese standard and scientific names and reading comments, it is possible that the children might have understood that their names for plants were fair and sensible.

First, children form vernacular names, then learn Japanese standard names and finally scientific names. This is an effective strategy to learn about plants. It was an interesting activity for the children to name a plant on their own since they exhibited such behavior as part of their own culture all across Japan around 60 years ago. This plant naming program may be effective in re-creating the children's culture that is presently lost. Furthermore, a method to learn common scientific names more easily is warranted.

2) The environmental awareness and its transformation on biodiversity conservation and maintenance at university campus ELF: N, Co, L

Since 1946, Tokyo Gakugei University's campus in Koganei-shi, Tokyo has supported diverse plant and animal life, including tall trees and crating splendid biotope networked to metropolitan parks. This area, recently named "Gakugeinomori," is managed by Gakugeinomori Environment Organization (GEO), a consultative body comprising students, faculty, staff, and local residents. GEO is responsible for publishing an annual environmental report, discussing campus environmental comfort and advising improvements.

GEO conducted a survey of campus stakeholders, revealing that most respondents had a favorable impression of the campus and its name but were largely unaware of GEO's conservation activities. Particularly, the students showed less interest in natural environment of the campus than the other attributes. To address this, practical conservation activities were introduced in lectures, such as collecting garbage, creating trails, and transplanting wild plants. These experiences helped students appreciate the value and skills of conservation, with cooperative activities enhancing environmental awareness and biodiversity appreciation. The cooperative activities enhance the students' environmental awareness on the biodiversity (Kimata and Saito 2013).

3) Lecture Courses Applying the ELF Environment Learning Process ELF: W

Undergraduate and graduate courses, including participants from Thailand, applied the ELF Environment Learning Framework, integrating ten programs for environmental learning. The Process has been proposed as a framework integrated ten programs for learning the environment. Students were asked to share association and impression of word , such as "nature," "environment," "environmental issues," and "hopes of topics" and related topics after classes. The answers were processed using SPSS Text Analytics for Surveys.

The students recognized "nature" as vast nature as forest, ocean, river and mountain, but these were not the familiar nature in their side. The student also recognized "environment" and "environmental issues" were seen as negative phenomena tied to global problems. Thai student regarded "nature" and "environment" as familiar and positive, whereas "environmental issue" was perceived negatively. Post-course, students broadened their understanding and added positive images to their conceptions, demonstrating the effectiveness of the ELF Environment Learning Process in fostering holistic environmental understanding. (Kimata et al. 2013).

4) Environment Learning Process and Need of “Environment Studies” ELF: W

“Environment learning” is fundamentally about developing one’s individual aptitude in relation to their living environment. In the modern ear, ongoing environmental learning is essential due to increase complexity. Leaners must integrate both scientific knowledge from formal education and traditional firsthand experience from the community. The environment learning process contains the flow of thinking from plain feeling to integrated intuition via analysis and synthesis.

The status of the environmental education was analyzed. Analysis of reports, including those from the GLOBE Program and the journal “Environmental Education,” as well as seminar summaries, indicated that environmental education in schools often overemphasizes science and lacks perspective, especially in elementary and secondary education. Many experts support the establishment of “environment studies” as a new, integrated school subject, combining knowledge from other subjects with comprehensive learning, fieldwork, and outdoor activities.

5) Popularization of Millets and Indigenous Varieties ELF: M, C

The Millet Straß is a network route of villages where farmers cultivate traditional millet species in Kanto Mountains, including sorghum, finger millet from Africa, foxtail millet, common millet from Central Asia, and Job’s tear from Southeast Asia and Japanese barnyard millet. These millets are endangered despite the very long cultivation history in Japan. Millets are nutritious grains that can grow under harsh environments. FAO had held the International Year of Millets in 2023 to re-evaluation those orphan crops. Common millet continues to grow throughout the Eurasia. Foxtail millet is a sacred cereal in India, Formosa, Okinawa, and the Japanese mainland (Kimata 2023).

Epilogue Monoculture of the mind and the self-domestication in Anthropocene, Quaternary

Shiva (1993) posits that diversity, uniformity, and productivity are interconnected within the agricultural systems. Higher yields have been pursuit to introduce uniformity and the logic of assembly line. The imperative of growth generates imperative for monocultures. Sustainability, diversity, and decentered self-organization are associated with one another, as are unsustainability, uniformity, and centralization.

The concept of 'monoculture of mind' (Shiva 1993) was a pioneering idea on 'self-domestication' (Wrangham 2019). Stout (2005) introduces the concept of conscious as the "seventh sense." Stout explained that conscience is an invisible yet persistent aspect of our being. However, much of what we do that looks like conscious is motivated by fear, social pressure, pride, and even simple habit. Conscious is neither behavioral nor cognitive, rather, it exists primarily in the realm of affect, better known as emotion. Conscious does not exist without an emotional bond to someone or something, and in this way, it is closely allied with love. If the first five senses are the physical and the sixth is how we refer to our institution, then conscious can be the seventh sense developed later in the evolution of our species and is still far from universal. The anonymity of evil and its maddening refusal to attach itself reliably to any particular social role, racial group, or physical type has always plagued theologians and, more recently, scientists. Throughout history, numerous efforts have been undertaken to define good and evil and to explain those among us who appear to be inhabited by such qualities. Genuine consciousness can promote peace, oppose hatred, and save lives; however, it is not possessed by everyone.

I categorize the characteristics of good supporting or evil inhibiting as the seventh sense (Table 64, Figure 112). If the seventh sense developed later in the evolution of our species and remains far from universal, the conscience would remain immature (Stout 2005). It involves obtaining good and evil. From another point of view, the seventh sense regressed evolutionally by the self-domestication in Anthropocene. If someone is self-centered and self-preserved, they are generally selfish.

Table 64. Good vs evil in the seventh sense

Good	vs	Evil
consideration		jealousy
sincere and earnest		envy
fairness		self-preservation, personaal gain, and selfish desires
know your suffciency		dissatisfaction
truth, goodness, and beauty		honor, power, money
discussion, empathy, compromise		restrictions on freedom of speech
nonviolent, disobedience		violence, suppression
liberty, equality, fraternity		rule of law, discrimination
faith		religion
peace		war
individual, family		group （*mure, mura, shima*）, local community, city state

Figure 112 presents a tree analogy to explain the formation of diverse character. We make progress numerous individualities under a certain era, such as Anthropocene. A human can grow, based on societal influence into “big tree,” or “small tree.”

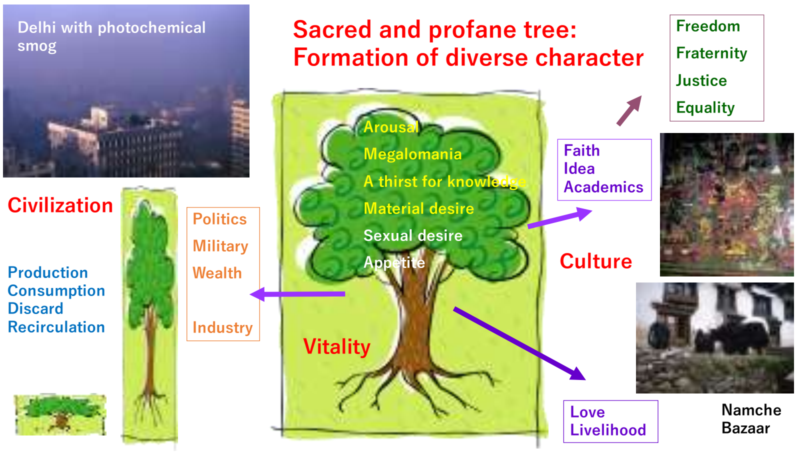

Figure 112. Development of diverse character through an analogy to a tree

Ancient sayings such as “Learn from the past 温故知新,” “Continuity and change 不易流行,” and “Contentment through learning 吾唯足知” provide enduring guidance. *Kakabhushundi*, the Crow hermit from the Ramayana’s fourth period (*Kalyug* Era), described a time of constant unrest, hostility, harmful thoughts, resentment, fear, and suffering. In such challenging times, all beings can transcend hardship by celebrating the deeds of Lord Hri (Vishnu). Although spiritual practices have waned in this age of decline, pure faith continues to bring abundant blessings. Living with a clear conscience enables one to attain liberation (moksha) without karmic suffering.

Valuable lessons can be drawn from India’s traditional ways of life. While adopting aspects of Artificial Intelligence (AI), it remains essential to cultivate Natural Intelligence (NIn), care for shared social resources, and acknowledge the rights of nature (Nash 1987). The *Chipko* movement in northern India serves as additional guidance for contemporary society. Today, the Anthropocene is marked by intense natural and artificial challenges, including climate change, disasters, diseases affecting humans and animals, AI-driven information technology, conflicts, and wars. These circumstances endanger global food security and overall well-being. Nevertheless, it is vital to maintain hope for future generations—children, youth, and all people.

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