

CHAPTER 1

Literature Review

1.1 *Oryza* genus

The genus *Oryza* originated in the Gondwanaland continents and, following the fracture of the supercontinent, became widely distributed in the humid tropics of Africa, South America, South and Southeast Asia, and Oceania (Chang, 1976). The genus *Oryza*, contains 20 wild relatives of the two domesticated species, are largely distributed in the humid tropics of Africa, South and Southeast Asia, south China, South and Central America, and Australia (Vaughan *et al.*, 2003). The genus is divided into four species complexes: the *O. sativa*, *O. officinalis*, *O. ridelyi* and *O. granulata* species complexes. All members of the *Oryza* genus have $n = 12$ chromosomes and while interspecific crossing is possible within each complex (Vaughan *et al.*, 2003).

The *O. sativa* complex contains two domesticated species: *O. sativa* and *O. glaberrima*, and five or six wild species: *O. rufipogon*, *O. nivara* (also considered to be an annual ecotype of *O. rufipogon*), *O. barthii*, *O. longistaminata*, *O. meridionalis* and *O. glumaepatula*, all of which are diploids with AA genome. *O. sativa* is distributed world wide with a high density in Asia, while *O. glaberrima* is grown only in West Africa. *Oryza rufipogon* can be found throughout Asia and Oceania. *Oryza barthii* and *O. longistaminata* are African species, *O. barthii* endemic in West Africa and *O. longistaminata* is found throughout Africa. *Oryza meridionalis* is native to Australia and *O. glumaepatula* is endemic in Central and South America. Given these

distributions, it is easy to locate the ancestral pools from which modern rice were originated. The African cultivars were domesticated from *O. barthii* (formally called *O. breviligulata*) (Semon *et al.*, 2005) and *O. sativa* was domesticated from *O. rufipogon* (Oka, 1988).

1.2 *Oryza sativa* primary gene pool

Nomenclature of genus *Oryza*, in particular that of wild relatives of the cultigens, is still in confusion to some extent. The classification of gene pools as suggested by Harlan and de Wet (1971) is useful to describe genetic relationship between cultivated rice and their wild relatives. They partitioned the whole variation range genetically reached by cultigens into three categories (Harlan, 1992): primary gene pool (races yielding reasonably fertile hybrids with cultivars), secondary gene pool (races crossable with cultivars but gene flow is restricted), and tertiary gene pool (crosses with cultivars are difficult, and gene transfer is not possible without special procedures).

According to the classification of gene pools, *O. sativa* and *O. rufipogon* belong to the same biological species and form a primary gene pool. Similarly, *O. glaberrima* and *O. barthii* form another primary gene pool. Therefore, *Oryza sativa* primary gene pool consisted of cultivated rice (*Oryza sativa*), its wild ancestor (*Oryza rufipogon* Griff.), and weedy form (*Oryza sativa* f *spontanea*) (Harlan, 1992).

1.2.1 Common wild rice

Common wild rice (*Oryza rufipogon* Griff.), the wild ancestor of Asian cultivated rice (*Oryza sativa* L.), is widely distributed in the tropics and subtropics of Asia described by Oka in 1988 and is the most important genetic resources for rice breeding since they share the same genome and are cross compatible with cultivated

rice. This wild ancestor exhibits unique some morphological characteristics but variation in life-history traits, mating system and habitat preference showing a differentiation into two ecotypes, perennial and annual types (Oka, 1988).

Perennial and annual types

Populations of common wild rice vary between the perennial and annual types. They differ in various life-history traits (Oka, 1988). Generally, the annual type is earlier flowering and has shorter culms, shorter ligules, shorter anthers and longer awns than the perennial type. Annual type are found in the shallow swamps, near rice field, roadside which become parched in the dry season and is generally non photoperiod sensitivity and mostly self pollination and propagated by seed. Perennial type are found in deep swamps or canals which retain soil moisture throughout the year and is generally sensitive to photoperiod, flowering once a year at the end of the wet season and mostly out crossing and propagates not by seed but by vegetative component call “perenniality”. Besides a difference in life-history traits, annual and perennial type, wild rice also differ in their mating system. The outcrossing rate in annuals was estimated as 16.6% to 33.9% and as 44% in perennial strain (Barbier, 1989b).

There is still continuing debate over species classification whether the perennial type was classified as *O. rufipogon* or the annual type was classified as *O. nivara*, however, in this study I would consider and refer to both the annual and perennial forms as common wild rice (*O. rufipogon*) due to Oka (1988) and Barbier (1989a) considered as the same biological species since they are interfertile.

1.2.2 Weedy rice

Weedy form or weedy rice (*Oryza sativa* f. *spontanea*) of the Poaceae is a weed accompanying rice and is widely distributed in rice-planting areas all over the world, particularly in South and South-east Asia, South and North America, and southern Europe (Noldin, 2000; Vaughan *et al.*, 2001; Gealy *et al.*, 2002). Weedy rice is taxonomically classified as the same species as cultivated rice (*Oryza sativa*), but strongly characterized by its seed shattering and dormancy (Cao *et al.*, 2006). Morphologically, weedy rice is highly variable and appears to be an intermediated between wild and cultivated rice. They display a range of undesirable agronomic traits damaging both cultivated rice yield and quality. Long-term sympatric distribution has led to similarities between weedy and cultivated rice through natural hybridization and introgression, making the control of weedy rice very difficult when compared with other weeds (de Wet and Harlan 1975).

Origin of weedy rice

There are three possibly evidenced of weeds originate within the man-made habitat (de Wet and Harlan, 1975): 1) from wild colonizers through selection towards adaptation to continuous habitat disturbances; 2) as derivatives of hybridization between wild and cultivated species; 3) from abandoned domesticates through selection towards a less intimate association with man. However, weedy rice in Thailand (*Oryza sativa*) is evidenced originate from interspecific hybridization between common wild rice (*Oryza rufipogon*) and Asian cultivated rice (*Oryza sativa*) (Niruntrayakul, 2007) as their flowering period overlaps, through the time of flowering peak of wild rice is either earlier or later than the cultivated rice (Chitrakon, 1995). Such hybridization between cultivated rice and common wild rice is a

common occurrence where they are coexist (Oka, 1988, and Song *et al.*, 2006) which is consistent with Ellstrand *et al.* (1999) pointed that the occurrence of hybridization between crop-wild ancestor complexes is more frequent. Consequently, weedy rice mostly found within cultivated rice field, abandon rice fields especially in the area where wild ancestor were found nearby the cultivated rice fields (Vaughan *et al.*, 2005).

Adaptation-crop mimicry

Weedy rice tends to mimic the growth attributes of the cultivars with which it grows, germinating simultaneously and growing at a similar rate, although earlier maturity is not uncommon (Baker, 1974). This mimicry is likely to be due to their origins in hybridization between those cultivars and the wild species. Populations of weedy rice tend to be genetically diverse and highly heterogeneous (Cheng, 2003). They have a high seed shattering rate and buried seeds with germinate with the crop the following season. In addition, their seeds can contaminate farmers' seed stocks and be sown with the cultivar each season. When weedy population grows sympatrically with cultivated species and hybridization occurs, cultivar genes may be added to the gene pool of the weedy populations by introgressive hybridization (Cao *et al.*, 2006). Further, this additional genetic material may promote the persistence of the weedy populations in cultivated habitats by allowing the weeds to become more adapted to man-made habitats and increased their weediness.

1.2.3 Cultivated rice

Asian cultivated rice is classified into two subspecies, *japonica* and *indica*, with a third group *javanica* classified as the tropical component of the subspecies *japonica* (Oka 1988). Many evidences suggest that the two primary subspecies are

the products of independent domestication events from the ancestral species, *O. rufipogon*, a hypothesis initially based on studies of biochemical traits (Second, 1982) and hybrid sterility and subsequently supported by molecular analyses (Cheng *et al.*, 2003). Recently, Londo *et al.* (2006) reported that *O. sativa indica* have been evidenced domesticated within a region south of the Himalaya mountain area including eastern India, Myanmar, and Thailand while *O. sativa japonica* was domesticated in Southern China by using sequence of the *atpB-rbcL*, *p-VATPase* and *SAM* genes. The genetic diversity of *japonica* and *indica* has been investigated based on morpho-physiological traits, isozymes, and nucleic and cytoplasmic molecular markers, and in these studies it was reported that genetic diversity was higher in *indica* than in *japonica*.

Landraces variety

Landraces population believed to be the intermediated stage in the domestication process from wild ancestor to elite variety (McCouch, 2004 and Londo *et al.*, 2006). Landraces have a certain genetic integrity (Harlan, 1992). They are recognizable morphologically; farmers have names for them and different landraces are understood to differ in adaptation to soil type, time of seedling, date of maturity, height, nutritive value, use and other properties. They are highly heterogeneous, having been selected for subsistence agricultural environments where low, but stable yields were important and natural environmental fluctuation required a broad genetic base (McCouch, 2004). Therefore, landrace populations are balanced, integrated mixtures of genotypes adapted to a region and to cultural practices in vogue (Harlan 1992). They are not adapted to high fertility, high plant populations, or high production, but their dependability makes them useful in difficult or marginal

situations. The great variability of landraces makes them good sources of genes for modern plant breeding.

1.3 Rice ecosystem

Through domestication, *O. sativa* has evolved into many different cultivars and ecotypes that are adapted to the wide range of conditions found in rice growing regions. Rice is grown from sea level to 3,000 m and in both temperate and tropical climates. A variety of water regimes are used, including moderately submerged lowland rice (irrigated or rain-fed), unsubmerged upland rice, and submerged rice. Four major ecosystems are generally recognized as follows (Khush, 1997): (1) Irrigated, (2) Rainfed lowland, (3) Upland, and (4) Floodprone.

1.3.1 Irrigated

Approximately, 55% of the world rice area planted to rice, is irrigated and is the most productive rice growing system. Perhaps 75% of the world rice production comes from irrigated areas and Asian mega cities are fed from irrigated rice (Khush, 1997). Most of the irrigated areas are planted improved or modern varieties and more fertilizer and other inputs are used than in other ecologies.

1.3.2 Rainfed lowland

About one-fourth of the world rice area is rainfed lowland (Khush, 1997). Rainfed lowland have a great diversity of growing conditions that vary by amount of rainfall and duration of rainfall, depth of standing water, duration of standing water, flooding frequency time of flooding, soil type and topography. Rice grown in this condition is faced with the fluctuation environment, therefore rice varieties growing in this ecosystem mostly are improved traditional varieties.

1.3.3 Upland

Upland or dryland rice is grown under rainfed, naturally well drained soils in banded or unbanded fields without surface water accumulation, aerobic soil. Some of the upland rice areas are on sloping mountain sides with low pH soils and deficient in nutrients. Rice varieties are photoperiod insensitive, have deep roots and some level of drought tolerance. Rice is planted under dry conditions thus, most of the upland areas are planted local or landrace upland varieties.

1.3.4 Floodprone

Floodprone or submerged rice is grown in low lying lands in river deltas of South and Southeast Asia. Standing water depth may vary from 50 cm to more than 3 m. However, flooding occurs only during part of the growing season. Rice growing in the floodprone ecosystem is landrace or improved traditional varieties.

Rice ecosystem in Thailand

Rice growing ecosystems in Thailand are basically differentiated related to water and temperature regimes (Rerkasem and Rerkasem, 2002).

1) **Upland rice** is grown on dry soil. It is found from about 1,000 m in elevation in the northern part (up to 20°N) of the country down to just a few hundred meters further south (to about 14°N).

2) **Mountain wetland rice** is grown in flooded soil, with water depth of 20-30 cm, in highland valleys and terraced fields at 600>1,000 m in elevation.

3) **Irrigated rice**, for which the water depth can be controlled at 20>30 cm, accounts for some 25% of the country's lowland rice land.

4) **Lowland rain-fed rice** is grown on relatively flat land, 400 m in elevation or lower, without water control. Drought is the primary constraint.

5) **Deep water and floating rice** is grown in low-lying areas where water depth may reach several meters.

6) **Dry season rice**, grown where there is water for irrigation, from January to June.

1.4 Evolution of *Oryza sativa*

Cultivated plants were domesticated from their wild progenitors about 10,000 years ago (Harlan 1992). Therefore, cultivated plants are genetically similar to their ancestral wild species but, although they belong to the same biological species, they show marked morphological differences which have been collectively called the domestication syndrome.

1.4.1 Domestication process

In the first phase of domestication, plants selected for cultivation were indistinguishable from their wild relatives. Once agriculture became established, humans selected traits that were useful with cultivated plants diverging from their wild relatives (Ellstrand *et al.*, 1999). Many phenotypic differences are obvious between *O. sativa* and its wild relatives (Xiao *et al.*, 1998; Cai and Morishima, 2002; and Li *et al.*, 2006). Sweeney and McCouch (2007) have summarized typical domestication traits during domestication process from wild rice to domesticated rice. Wild rice typically display long awns and severe shattering for seed dispersal, whereas the domesticated type have short awns if any and reduced shattering to maximize the number of seeds that can be harvested (Li *et al.*, 2006). Dormancy levels are higher in the wild rice, allowing viable seeds to persist for years before germination, but these have been reduced in cultivars to give uniform germination (Gu *et al.*, 2006). The pericarp and seed coat of wild grains contain a pigment giving them a red colour

which modern Asian cultivars lack (Gealy *et al.*, 2002). Seeds hulls are straw coloured in the domesticated but dark in the wilds. Mating habits differ, *O. rufipogon* is partially outcrossing, with estimates ranging from 10 to 50 %, while *O. sativa* is almost entirely inbreeding (Oka 1988). Wild grains are consistently small while domesticated grains vary in size. The panicle structure has changed from an open panicle with few secondary branches bearing relatively few grains, to a densely packed panicle that can carry larger numbers of seeds than the wild ancestors (Oka 1988).

1.4.2 Wild-weed-crop complex

Genetic compatibility between wild and domesticated populations leads to wild-weedy-domesticated complexes in sites with sympatric distribution by introgression of genes from wild populations to domesticated ones or vice versa (Zizumbo-Villarreal *et al.*, 2005). Naturally occurring outcrossing in original habitats among wild, weedy and domesticated or cultivated rice during the ongoing domestication could result in gene flow among the several biological components of a complex. As weedy types arise from crosses between cultivated and wild forms, therefore weedy types may in turn both derive and contribute genetic diversity in relation to wild and cultivated types. In fact, a genetic composition in the form of hybrid swarm may result among the various types, and such hybrid swarms may be generated repeatedly over time (Beebe *et al.*, 1997). The resulting hybrid swarm might evolve towards the wild forms under natural selection pressure (thus the terms de-domestication or regressive forms); conversely if human driven selection is exerted, either directly on the plant material itself, or indirectly by significant modification of the environment the hybrid swarm will progressively include only crop-like

components (Beebe *et al.*, 1997). If farmers can benefit from the variants so generated, the presence of a wild-weed-crop complex might be indicative of a place of ongoing domestication activity.

1.4.3 Landrace populations

Landraces of rice are thought to be an intermediate stage in the process from wild ancestor to cultivated rice in the domestication process. *Oryza sativa* has evolved into many different cultivars that are adapted to the wide range of conditions found in rice growing regions world wide. In addition, they represent a unique and critical source of genetically variable traits that can serve as a resource for future rice improvement. Generally, landraces evolved at low levels of cultivation, fertilization and plant protection, subject to selection pressures for hardiness and dependability rather than for productivity. That genetic diversity within landraces provided some protection against climatic extremes and epidemics is plausible. The components of landraces often are deliberately manipulated by local farmers. While landraces may under some conditions have lower yields than modern varieties in many crop growing areas in the world, farmers may favor landraces because they are better adapted to local conditions and are specific for regional uses of rice (Parzies *et al.*, 2004). The genetic variability found within landraces affords the possibility of genetic flexibility; landraces have the potential to adapt to the local field conditions and they can adapt to changing environments, farming practices, and specific uses such as animal versus human consumption (McCouch, 2004). The genetic structure of landrace populations is affected by processes that are not significant for high yield crops. Among the factors influencing genetic structure and diversity of landrace populations are the population genetic processes of drift, selection, and mating system. In addition to

these “natural” process, the management practices of local farmers have an extremely strong influence (Parzies *et al.*, 2004).

1.4.4 Genetic diversity

1.4.4.1 Common wild rice

Common wild rice, *Oryza rufipogon* Griff., is widespread in number of Asian countries including China, Laos, Thailand, Myanmar, Nepal, Bangladesh, Taiwan, Vietnam, Cambodia, Indonesia and India, keep different varieties in local populations. However, common wild rice population in Taiwan has been reported disappear in 1978 (Song *et al.*, 2005). Populations of common wild rice contain far more genetic variation than does cultivated rice, based on morphology, allozymes and DNA markers. However, little information is available on how genetic diversity is structured within common wild rice populations. Moreover, study areas of common wild rice are mostly in mainland China. Gao (2000a) has examined the genetic diversity of Chinese common wild rice (*O. rufipogon*) populations using the allozyme method, Ge *et al.* (1999) have compared RAPD variation of Chinese common wild rice with that from Brazil, Song *et al.* (2003, 2004), Zhou *et al.* (2003) and Gao (2002, 2004) assessed wild rice populations in China using SSR markers. In average, genetic diversity of common wild rice in China is in range of 0.493 – 0.708. Therefore, a comparison of levels of genetic diversity among *Oryza* species, reported using different marker systems, suggested that *O. rufipogon* maintains high genetic variation within populations.

The knowledge of genetic structure and genetic diversity of natural populations of common wild rice (*O. rufipogon* Griff.) in Thailand is limited and were studied only a few workers. Morishima and Oka (1970) analyzed quantitative traits of

common wild rice population in Thailand while Barbier (1989a; 1989b) and Morishima and Barbier (1990) were study life-history traits and genetic diversity using allozymes markers. Recently, Punyalue (2006) assessed morphological variation and genetic diversity of 12 common wild rice populations. The results indicated that common wild rice populations in Thailand were classified into 3 types; perennial, intermediate and annual by morphological characters. Genetic diversity was assessed using 7 microsatellite loci showed that total gene diversity (H_T) over all twelve populations was 0.225. In addition, Wongtamee (2008) found that 37 common wild rice populations in Thailand were also classified in to three types; annual, intermediate and perennial types based on five microsatellite markers and showed moderate to high level of gene diversity.

Hamrick and Godt (1996) have pointed that genetic diversity maintained by a species is a function of its ecological and evolutionary history. For *O. rufipogon*, it is likely that the extensive geographical distribution, mixed mating system (Morishima and Barbier 1990), historically large population sizes and diverse reproductive strategies (Gao *et al.* 2000b) have contributed to the high levels of genetic diversity of common wild rice species.

1.4.4.2 *Cultivated rice*

Through domestication, *Oryza sativa* L. has evolved into many different cultivars that are adapted to the wide range of conditions such as different water regimes and wide range of soils that could be found in rice growing regions world wide (Oka, 1988). A large number of *O. sativa* cultivars have been developed in primitive agriculture by human and natural selection, over a long period of time and they remain relatively unmodified, despite generations of selection by farmers and

have become adapted to different human and environmental influences (Sanni *et al.*, 2007), they are called landraces cultivars.

The cultivation of landraces rice varieties in Asia has been declining since the beginning of the Green Revolution (Harlan 1992) by the replacement of high yielding varieties or modern rice varieties. Modern rice varieties generally have significantly higher yields than traditional varieties or landraces varieties when grown under controlled conditions, with relatively stable sources of water and a sufficient supply of inputs (Khush 1997). Modern variety population structure is totally differing from landraces or traditional populations. Modern varieties show homozygous genotype and homogenous population whereas landraces or traditional varieties show mixed homozygous and heterozygous genotype and they are all heterogeneous population. Modern varieties show no variation within variety due to the fixation of various loci during selection process of breeding program, but exhibit high level of genetic differentiation among varieties due to different genetic background sources. In contrast, landraces rice varieties show genetic differentiation within variety and high level of differentiation between varieties.

1.5 Evolutionary forces on crop population structure

The genetic structure of a population of organisms, and ultimately the establishment of independent evolutionary lineages, is strongly influenced by the pattern of genetic exchange within and between populations (Schaal *et al.*, 1998). Evolutionists believe that they have a satisfactory understanding of the nature of the processes leading to population differentiation at the intraspecific level. They consider mutation, selection, migration and drift, as well as factors related to the

organization of the genetic material, sufficient to explain the phenomena of population differentiation (Sokal and Wartenberg 1983).

1.5.1 Plant population genetic structure

Plant populations are not randomly or uniformly but they are distributed in space and time (Loveless and Hamrick 1984). This structure may be manifested among geographically distinct populations, within a local group of plants, or even in the progeny of individuals. Genetic structure results from the interaction of mutation, migration, selection, and drift, which in turn must operate within the historical and biological context of each plant species. Ecological factors affecting reproduction and dispersal are likely to be particularly important in determining genetic structure (Loveless and Hamrick 1984).

Diversity is expressed as genetic differences between species, subspecies, varieties, populations or individuals. Diversity may be measured at the morphological level, physiological level and also can be measured in term of differentiation in biochemical, protein and molecular (DNA) levels within and between plant populations. The amount of genetic diversity differs between populations or between regions and localities, and several key factors determine its distribution (Loveless and Hamrick 1984).

1.5.2 Spatial variation

Spatial genetic structure - the non-random distribution of different genotypes – is a product of the genotypic diversity present and a significant factor affecting how that diversity is maintained. Assuming that genetic variation is present, plant populations generally exhibit some level of genetic structuring unless gene flow is entirely unrestricted (Wright 1943), however, detecting it will depend on the resolving

power of the system used to differentiate genotypes and on sufficient statistical sensitivity (Smouse and Peakall 1999). The spatial scale of sampling also determines whether genetic structuring is detected and at what level.

Spatial structuring can strongly influence, and be strongly influenced by, most other important aspects of population genetics, including mating system, individual fitness, inbreeding, and the action of various forms of natural selection. Spatial and geographic patterns of genetic variation have been a subject traditionally of great interest to geneticists (Gray, 1996).

Isolation by distance

The term “isolation by distance” (IBD) was first used by Sewall Wright to describe patterns of population genetic variation that derive from spatially limited gene flow (Wright, 1943). IBD is defined as a decrease in the genetic similarity among populations as the geographic distance between them increases. Isolation by distance results from less mixing among individuals, or pairs of populations, which are situated further apart than among those which are separated by shorter distances (Palsson 2004). This leads to a positive correlation among genetic and geographical distances, either within a continuously distributed species or among populations with discrete structure (Kimura and Weiss 1964).

1.5.3 Temporal variation

Linhart and Grant (1996) pointed that a temporal constituent is relevant to fine-scale differentiation in two contexts. One is to determine rates of evolutionary change by time. The other is that rapid changes in environmental conditions can expose different cohorts within a population to different selection pressures, thereby generating temporal differentiation in genetic constitution. However, many factors

influenced temporal variation pattern of plant population in the context of life-history traits, mating system, different geographical scale, different conditions of light, moisture, competition, and other factors, so different genotypes are selected.

For example, different patterns of genetic variation between populations within a species over time due to the variation rates of outcrossing and selfing which may be dependent on geographical or seasonal variation in the distribution of pollinators (Schaal *et al.*, 1998). Population structure of landraces Sorghum in Northern Cameroon showed different pattern of landraces sorghum which was the consequences of history which is vary in the time since they were introduction into the village which more recently introduced landraces are genetically more distinct (Barnaud *et al.*, 2007). In addition, population history is also a determinant factor of the genetic variation within species (Schaal *et al.*, 1998). Population history, represented as fluctuations in the number and size of populations, and the evolutionary and biogeographic histories of species, may have played critical roles in determining its current genetic composition (Schaal *et al.*, 1998).

1.5.4 Selection

Selection is the primary force that shapes the levels and patterns of genetic diversity within and between populations. Selection happens when certain individuals in the population are more likely to survive to maturity and produce more offspring than other individuals. Selection often changes the frequency and genotypes or alleles during the course of one generation. Intense selection may sometimes be operative but not necessarily with any generational change in these frequencies. Selection arises both from the deliberate choices of the farmer and from the agricultural, biotic and abiotic environment (Ouborg *et al.*, 1999).

Correlation between environmental heterogeneity and genetic variation has been documented for many species and at multiple scales (Ward, 2006). Environmental heterogeneity contributes to genetic structuring through two forces (Ward, 2006), often interesting synergistically. First, environmental barriers may restrict gene flow, increasing genetic differentiation among populations or subpopulations. Second, environmental heterogeneity may result in genetic structuring through the exertion of different selection pressures. For example, genotypic differentiation resulting from selection for heavy metal tolerance has been documented in plant population over distances from a few centimeters to many kilometers (Mengoni *et al.*, 2000). Both phenomena occur at a wide range of spatial scales. As a general rule, selection by biotic factors generates less clearly defined mosaics of genotypic distribution patterns than those resulting from physical factors, especially at smaller scales (Linhart and Grant 1996).

1.5.5 Gene flow/Migration/Seed flow

Gene flow occur when there is migration of individuals (e.g., seeds flow) or gametes (e.g., pollen flow) between populations (Ellstrand *et al.*, 1999). Along with drift, selection, and mutation, gene flow as well as seed flow represents one of the main evolutionary forces causing changes in gene frequencies of the populations. The main effect of gene flow is the reduction of differentiation between populations accompanied by a parallel increase in differences between individuals within a population. The life-history and demographic factors are also important in the determination of the effect of gene flow on the structure of genetic diversity (Savolainen *et al.*, 2007).

Gene flow between wild and domesticated populations is also limited by their phenology, geographic distribution, and spatial arrangement. Gene flow can occur if plant populations have overlapping flowering periods and are at a suitable distance, depending on the seed and pollen dispersal ability and the environment factors. Pollen and seed dispersal rates are strictly correlated with distance, such that dispersal rapidly decreases with distance to a very low value (e.g., within 50 – 200 meters), although a relatively low level of dispersal may occur even over very great distances (e.g., several kilometers) (Papa and Gepts 2004).

Evidence of gene flow between wild progenitors and domesticated crops has been documented in 13 world's most important food crop species (Ellstrand *et al.*, 1999). In some cases, hybridization between wild and domesticated populations leads to the development of weedy populations (Ellstrand *et al.*, 1999) that can be found in farmers' fields or that can colonize other disturbed environments and present intermediate characteristics between wild and domesticated forms.

1.5.6 Genetic bottleneck

Domestication has long been an area of great interest in the study of evolution (Darwin 1859) and believed to be that the major force reducing genetic variation of domesticated plants in comparison with their wild progenitor species (Tanksley and McCouch 1997; Doebley *et al.*, 2006). This reduction in genetic diversity has resulted partly from small initial populations in crops relative to their wild ancestors and partly from intense selection for agronomic traits (Eyre-Walker *et al.* 1998; Clark *et al.* 2004; Zeder *et al.* 2006). The former effect, often referred to as "domestication bottleneck" (Eyre-Walker *et al.* 1998), is featured by a genome-wide loss of genetic diversity, whereas selection is locus specific and occurs in regions of the genome that

are tightly linked to the sites that are the targets of selection (Clark et al. 2004; Zeder et al. 2006). Thus, knowledge of the process and dynamics of crop domestication is important, both because domestication bottlenecks limit genetic variation in crops (Eyre-Walker et al. 1998; Buckler et al. 2001) and because any approach that analyzes variation in populations should be based on population genetic parameters (Eyre-Walker *et al.* 1998; Liu and Burke 2006).

1.6 Farmers' management of socials' role

Natural occurrences, as well as human activities, can lead to phenotypic crop diversity within a given production system (Louette *et al.*, 1997). To understand the dynamics of local crop diversity, an interdisciplinary of population genetics, environmental and social aspects, farmers' own local knowledge, and the circumstances of their seed systems, are all integrated (Brown, 2000). By this approach, effective *in situ* conservation strategies can be developed that will prevent loss of diversity in farmers' fields and help sustain the processes of evolution, namely, the adaptation of crop to their changing environments (Brush, 1995). In communities, the crops and varieties that exist are part of an evolutionary process of cultivation by farmers to continually adapt to the changing environment and their needs. This was a result of the interaction between people and the environment (Soleri and Cleveland 1993). Farmers have created and managed the environment where plants could evolve under selective pressure. Their farming systems, crop and varieties adapted to different environments, thus creating a diversity of crops, varieties and agro-ecosystem.

Seed system/seed exchange/seed flow

Several studies recognized farmer's role in the management of diversity (Dennis, 1987; Bellon and Brush, 1994). Besides selection, mutation and recombination, seed flow which is a form of migration of germplasm into a locality, is one of the primary mechanisms through which new diversity enters farming systems. The seed systems adopted by farmers are crucial to the management of agricultural biodiversity (Almekinders *et al.*, 1994). Cultural traditional play an important role in mediating seed acquisitions, such as kinship networks and gender responsibilities for rice (Sirabanchongkran *et al.*, 2004). The research behind seed acquisition may include farmer experimentation and the perception of value in moving seed between fields. The term seed exchange refers to a reciprocal relationship in which a farmer acquires seed by giving seed to other farmers (Balma *et al.*, 2000). A farmer also may obtain seed through other means, such as gifts or payment in cash, grain, or another non-seed commodity or purchase of grain that is utilized as seed. Human migration, marriage outside the community, and outside job opportunities can play important roles in disseminating seeds over larger distances and across geographical or cultural barriers.

The genetic constitution of the varieties will also be influenced by seed exchange between farmers, villages or regions, and by the extent to which farmers mix exchanged seeds - or their progeny - either deliberate or accidentally. Seed and seedling survival ensuring storage, germination and emergence also will have significant effects on the genetic constitution of the next generation. Differences between seed parents in respect of their contribution to the farmers' variety can be measured as differences in fitness (Balma *et al.*, 2000).