# Population Genetics of Traditionally Cultivated Rice Varieties in the Eastern Himalayan Region of Northeast India 

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A thesis<br>in the<br>Department of Biology

Presented in Partial Fulfillment of the Requirements For the Degree of Doctor of Philosophy (Biology) at Concordia University

Montreal, Québec, Canada

July 2013

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# CONCORDIA UNIVERSITY <br> School of Graduate Studies 

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## Doctor of Philosophy (Biology)

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#### Abstract

Population Genetics of Traditionally Cultivated Rice Varieties in the Eastern Himalayan Region of Northeast India

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The Eastern Himalayan region of northeast (NE) India covers a geographical area of over 255,000 sq. km. and consists of Arunachal Pradesh, Assam, Manipur, Meghalaya, Mizoram, Nagaland and Tripura states (Figure 1.1). This region encompasses wide range of eco-geographical conditions, ranging from lowland flood plains of Brhamaputra and Barak River to mountains as high as 4000 m above sea level in the West Kameng and Tawang region of Arunachal Pradesh. Rice (Oryza sativa) is the staple food of the local inhabitants in NE India. Traditional farmers of the region cultivate a large number of indigenous rice varieties under diverse topographic and agroclimatic conditions and different growing seasons. However, rice genetic resources in NE India are being rapidly lost due to changes in the land use and agricultural practices that favor agronomically improved varieties. A detailed understanding of the genetic structure and diversity of rice varieties in NE India is crucial for developing conservation and management strategies of rice genetic resources and use of the rice gene pool in the region for breeding and genetic improvement programs.

In this study, genetic structure and diversity of rice varieties representing several ecotypes collected from various regions of NE India were investigated using molecular tools. Chapter 1 covers a study focused on the genetic structure and diversity of 24 indigenous varieties representing Sali (12), Jum (4), Boro (3), and glutinous (5) types and
five agronomically improved varieties. The results revealed that the genetic diversity among indigenous rice varieties was higher than that of the agronomically improved varieties. The Sali and Jum types showed significantly higher levels of genetic diversity as compared to agronomically improved types. Two major genetically distinct clusters were detected in this study, which corresponded to two subspecies of $O$. sativa, namely indica and japonica.

In Chapter 2, the results of a study on characterization of rice ecotypes into japonica or indica subspecies using insertion-deletion (indel) markers are presented. The indel markers were designed based on the genome-wide DNA polymorphism database of typical indica cv 93-11 and japonica cv Nipponbare. The result showed that the traditional method of indica and japonica rice classification based on cultivation type, morphological traits, physiological and biochemical characteristics is incongruent with the indel marker based classification. Majority of the upland (Jum) and glutinous seeded varieties, which were traditionally classified as japonica clustered with indica types. Similarly, a few lowland varieties, which were traditionally classified as indica clustered with japonica types.

Chapter 3 covers the nucleotide polymorphism and patterns of nucleotide diversity at two trait specific genes, $W x$ and $O s C 1$. The $W x$ gene is associated with amylose content, which determines the glutinous nature of rice grains while the OsCl gene is associated with the apiculus coloration. The polymorphism in the $W x$ gene among glutinous and nonglutinous grain types, and the nucleotide diversity in the OsCl gene among colored and colorless apiculus rice varieties were investigated. The results revealed that trait specific nucleotide polymorphisms that were identified in previous
studies did not necessarily correspond to the specific phenotypes in the indigenous rice varieties of NE India. The glutinous type varieties showed higher levels of nucleotide diversity as compared to the nonglutinous types at the $W x$ locus. The neutrality analysis did not reveal signature of selection among the glutinous and nonglutinous rice phenotypes at the $W x$ gene. On the other hand, the $O s C 1$ gene revealed low level of selection among the colorless apiculus varieties as evident by lower nucleotide diversity in colorless types as compared to the colored apiculus varieties.

## ACKNOWLEDGEMENTS

I express my sincere appreciation to my supervisor Dr. Selvadurai Dayanandan for his valuable suggestions and guidance throughout the period of this project. His continuous effort, encouragement, endless support and wisdom greatly helped me in learning and understanding my research. I am indebted to him far beyond words.

I also express my sincere gratitude to my committee members and examiners Dr. Dan McLaughlin and Dr. William Zerges for their valuable comments that improved my thesis significantly. I gratefully acknowledge the guidance and support received from Dr. M.L. Khan (Department of Botany, Dr. Harisingh Gour Central University, Sagar, India) throughout the course of the study. His encouragement always helped me in moving forward with my research.

I would like to thank Concordia University and Natural Sciences and Engineering Research Council of Canada for financial support. I am especially indebted to the Le Fond Québécois de la Researche sur la Nature et les Technologies, the Faculty of Arts and Science and the Biology Department of Concordia University and the Graduate Awards Committee for granting their prestigious awards to me. I acknowledge the International Rice Research Institute, Philippine for providing samples for this study.

I give thanks to my lab colleagues, past and present members and especially Atiqur at the Forest and Evolutionary Genomics Lab. Assistance received from Sabrina and Kristiana are gratefully acknowledged.

I extend my special acknowledgement to my parents for support and care that greatly helped me to achieve this goal. Finally, words fail to express the appreciation and love to my wife Sabnam for her devotion, encouragement and endless support during the whole period. She is and will be my constant source of inspiration and motivation.

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## General Introduction

Asian cultivated rice (Oryza sativa L.) is one of the most important crops in the world and a major food source for over half of the global human population. Rice consumption data between 1961 and 2005 showed that about $20 \%$ of the daily calorie needs of the world population are met by rice (World Rice Statistics 2010). Rice is also the basis of food security in many developing countries and closely associated with cultural traditions and customs in local regions (Lu and Snow 2005). It is grown worldwide in diverse agroclimatic, edaphic and topographic conditions.
$O$. sativa is considered to have been domesticated from its wild ancestor, $O$. rufipogon by the Asian Neolithic farmers approximately 10,000 years ago (Normile 1997). Since its domestication, cultivated rice may have undergone significant genetic differentiation resulting in the evolution of several ecotypes, subgroups and varieties in various rice growing regions. A major differentiation of $O$. sativa resulted in two partially isolated gene pools referred to indica and japonica. These two major groups of varieties, also often referred to as subspecies, are distinguished on the basis of a number of morphological, physiological, biochemical and molecular traits (Oka 1988; Vaughan et al. 2008; Lu et al. 2009). A recent genome-wide study revealed that indica was domesticated in South and South East Asia while japonica was domesticated in Southern China (Huang et al. 2012). Further diversification of the $O$. sativa complex into at least five distinct groups such as indica, aus, aromatic, temperate japonica, and tropical japonica have also been reported (Garris et al. 2005). The combined effects of natural and human induced selection may have played a significant role in genetic differentiation leading to morphological discontinuity, genetic incompatibility and eventually the
evolution of different subspecies and diverse varieties (Wang et al. 1998). Cultural practices and consumer quality preferences may also have played a significant role in shaping the diversification of rice varieties.

## Plant domestication and trait diversity

Domestication refers to a process of selecting wild varieties of organisms with traits preferred by human needs (Darwin 1859). In other words, plant domestication is a process of genetic selection of wild species to meet human needs (Doebley et al., 2006). The most important domestication related traits identified so far in rice with significant morphological and physiological modifications are reduction in grain shattering (Konishi et al. 2006; Li et al. 2006a), changes in grain coloration (Sweeney et al. 2006), grain size and shape (Yamanaka et al. 2004), grain fragrance and flavor (Bradbury et al. 2005), grain number (Ashikari et al. 2005), grain weight (Song et al. 2007) and grain stickiness (Yamanaka et al. 2004). Synchronization of seed maturation, reduction in tiller number, increase in tiller erectness, increase in panicle length and branches, and reduction in awn length are also important traits related to domestication (Bres-Patry et al. 2001; Thomson et al. 2003; Li et al. 2006b; Sang and Ge 2007a).

During the domestication of crop plants, many traits of ecological and economic importance have been selected while others may have been lost. This is because early farmers selected seeds only from what they considered as the 'best' plants, which formed the next generation and much of the genetic diversity in the progenitor was left behind (Doebley et al. 2006). Estimates suggest that cultivated rice maintained less than $25 \%$ of the genetic diversity found in its wild progenitors, depicting a severe genetic erosion
during domestication (Zhu et al. 2007). Sakai and Itoh (2010) estimated loss of at least one thousand genes in cultivated $O$. sativa that are still preserved in the genomes of wild relatives. Out of the two major subspecies of rice, $O$. sativa ssp . indica is considered to maintain twice as much genetic diversity than $O$. sativa ssp. japonica, suggesting that the former had a larger founding population and/or may have been subject to a less severe bottleneck during domestication (Sang and Ge 2007a).

## The history of rice domestication

The history of rice domestication is complex and has been reviewed by many authors (e.g. Vaughan et al. 2005; Doebley et al. 2006; Kovach et al. 2007; Sang and Ge 2007b; Izawa 2008, Fuller et al. 2010; McCouch et al. 2012). The recent archaeobotanical evidence suggests that the process of rice domestication occurred in the Lower Yangtze region of Zhejiang, China (Fuller et al. 2009). Phylogeographic studies suggest that $O$. sativa ssp. indica was domesticated from wild rice progenitors in a region South of the Himalayan mountain range, likely Eastern India, Myanmar and Thailand, whereas $O$. sativa ssp. japonica was domesticated in and around Southern China (Khush 1997; Londo et al. 2006). This was further supported by a recent genome-wide study (Huang et al. 2012). In general, the geographic region of rice domestication is considered to have started from NE India extending eastward to Nepal, Myanmar and the Southwest corner of China in Yunnan Province (Chang 1976).

## Rice diversity in Northeast India

The diversity of traditional rice varieties in the Indian subcontinent is very high suggesting that this region may have played an important role in the domestication process of the crop. For instance, many studies show that the Jeypore tract of Orissa in Eastern India could be considered as a region that played a significant role in domestication of cultivated rice in India (Sampath and Govindaswami 1958; Oka 1964; Govindaswami et al. 1966; Akihama and Toshimitsu 1972). Similarly, the diversity of both indigenous varieties and wild relatives of rice is very high in the Eastern Himalayan region of NE India. The NE Indian region consists of seven states namely Arunachal Pradesh, Assam, Manipur, Meghalaya, Mizoram, Nagaland and Tripura (Figure 1.1) and covers an area of more than $255,000 \mathrm{sq}$. km . It is estimated that about 10,000 indigenous rice cultivars of agronomical, ecological and cultural importance are still preserved in NE India (Hore 2005). Such vast rice gene pools may possess many traits of agronomic and ecological significance.

Rice varieties cultivated at higher elevation areas (2,500-3,000 m asl) in the state of Arunachal Pradesh possess morphological features attributable to $O$. sativa ssp. japonica such as a globose grain, narrow, dark green and drooping flag leaves and a thin culm (Gupta et al. 1995). About 40\% of the 'Jum' (slash and burn agriculture) cultivated rice varieties in Nagaland state show morphological features intermediate between japonica and indica. Many rice varieties cultivated in Nagaland also show wide variation in grain size and shape, awn characters, glume and kernel color. Soft and sticky rice varieties are abundant in Meghalaya and at least 20 dominant landraces are still cultivated in Garo Hills district of the state. Lowland and deep water rice cultivation is common in Assam
with numerous scented, glutinous and colored grain varieties. The state of Mizoram is rich in aromatic and sticky rice as well as a few drought and cold tolerant varieties.

Jum cultivation is the main land use practice in the hill region of NE India (Ramakrishnan 2006). Rice varieties with special adaptations to upland areas are widely cultivated in such agricultural systems with no surface water accumulation. Jum rice varieties cultivated in the upland areas of South East Asia are considered as japonica type. On the other hand, farmers residing at low-lying flood plains of Assam and adjoining states cultivate different varieties of rice in different seasons. The two major growing seasons of this region are cold and dry seasons (Boro type during Nov to May) and hot, humid and rainy seasons (Sali type during Jun-Dec). The Sali type of varieties grown during the rainy season is the major crop having higher yield, better grain quality and superior agronomic traits. Traditional classification system categorized Sali type as typical indica type. These are widely cultivated throughout tropical Asia.

The other varieties, commonly known as Boro are traditionally cultivated during the winter season (January to April) in low-lying areas where sufficient water is retained during the cold and dry spells of the year. Boro rice may have some degree of cold tolerance because of their adaptation for winter conditions. In addition to the cultivated rice, natural populations of many wild rice species such as Oryza rufipogon, $O$. granulata, O. officinalis, O. nivara, O. meyeriana, Hygrorhiza aristata, Leersia hexandra and Zizenia latifolia are also found in the northeastern region of India (Hore 2005).

Introduction of agronomically improved varieties, changes in agricultural practices and habitat loss are posing serious threat to the rice gene pool of the region. Therefore, strategic conservation of such genetic resources is urgently needed. A detailed knowledge
of the levels of genetic diversity and genetic differentiation among different rice varieties in the Eastern Himalayan region is crucial for planning conservation, management and sustainable use of rice genetic resources in the region.

With this background, my study focused on investigating the population genetic structure of traditionally cultivated indigenous rice varieties in the Eastern Himalayan region of NE India. In Chapter 1, I report the results of a study focused on within and among variety genetic diversity and distribution of genetic diversity among different ecotypes and agronomically improved rice varieties from NE India using SSR markers. In Chapter 2, indica and japonica-specific insertion or deletion (indel) markers were used to identify the nature of genetic differentiation among different rice varieties or ecotypes in the region. In Chapter 3, I present the results of the analyses of DNA sequence variation of selected trait-specific genes in different phenotypic groups highlighting the nature of polymorphism and signatures of selection.

## Chapter 1: Genetic Structure and Diversity of Indigenous Rice (Oryza sativa) Varieties in the Eastern Himalayan Region of Northeast India


#### Abstract

The Eastern Himalayan region of NE India is home to a large number of indigenous rice varieties, which may serve as a valuable genetic resource for future crop improvement to meet the ever-increasing demand for food production. However, these varieties are rapidly being lost due to changes in land-use and agricultural practices, which favor agronomically improved varieties. A detailed understanding of the genetic structure and diversity of indigenous rice varieties is crucial for efficient utilization of rice genetic resources and for developing suitable conservation strategies. To explore the genetic structure and diversity of rice varieties in NE India, I genotyped 300 individuals of 24 indigenous rice varieties representing Sali, Boro, Jum and glutinous types, 5 agronomically improved varieties, and one wild rice species (O. rufipogon) using seven SSR markers. A total of 85 alleles and a very high level of gene diversity (0.776) were detected among the indigenous rice varieties of the region. Considerable level of genetic variation was found within indigenous varieties whereas improved varieties were monoporphic across all loci. The comparison of genetic diversity among different types of rice revealed that Sali type possessed the highest gene diversity ( 0.747 ) followed by Jum (0.627), glutinous (0.602) and Boro (0.596) types of indigenous rice varieties, while the lowest diversity was detected in agronomically improved varieties (0.459). The AMOVA results showed that $66 \%$ of the variation was distributed among varieties indicating a very high level of genetic differentiation in rice varieties in the region. Two major genetically defined clusters corresponding to indica and japonica groups were


detected in rice varieties of the region. Overall, traditionally cultivated indigenous rice varieties in NE India showed high levels of genetic diversity comparable to levels of genetic diversity reported from wild rice populations in various parts of the world. The efforts for conservation of rice germplasm in NE India should consider saving rice varieties representing different types with specific emphasis given to Sali and Jum types. The protection against the loss of vast genetic diversity found in indigenous rice varieties in NE India is crucial for maintaining future food security in the changing world.

Keywords: Conservation; Eastern Himalaya; Genetic diversity; Genetic structure; Indigenous rice varieties; NE India.

## Introduction

The Asian cultivated rice (Oryza sativa L.) is one of the most important crops and a major food source for more than half of the global human population. Phylogeographical and archeological evidence suggest that rice was domesticated over 10000 years ago from its wild ancestor $O$. rufipogon in the region south of the Himalayan mountain range, likely in the present day Eastern and NE India, extending Eastward to Nepal, Myanmar and Thailand to Southern China (Chang 1976; Khush 1997; Londo et al. 2006). A recent study suggests that one of the two subspecies of Asian rice, $O$. sativa ssp. indica was domesticated in Southeast and South Asia while the other subspecies, $O$. sativa ssp. japonica was domesticated in Southern China (Huang et al. 2012). During the domestication process, individuals with desirable traits have been selected leaving most of the genetic diversity behind in the progenitors (Doebley et al. 2006). Zhu et al. (2007) estimated that the cultivated rice contains only about $25 \%$ of the genetic diversity found in its wild progenitors depicting severe genetic erosion during domestication. Furthermore, a considerable level of genetic diversity was lost during the agronomic improvement of commonly cultivated rice.

Studies have shown that indigenous crop varieties traditionally cultivated and maintained by farmers contain high levels of genetic diversity and can serve as potential genetic resources for improving yield, resistance to pests and pathogens, and agronomic performance (Brush 1995; Hoisington et al. 1999; Mandel et al. 2011). The Eastern Himalayan region of NE India, a geographical area of over $255,000 \mathrm{~km}^{2}$ consisting of Arunachal Pradesh, Assam, Manipur, Meghalaya, Mizoram, Nagaland and Tripura states (Figure 1.1), is home to a large number of indigenous rice varieties. These varieties are


Figure 1.1: Map of northeast India showing sampling sites of traditionally cultivated indigenous rice varieties.
cultivated in diverse topographic and agroclimatic conditions, and normally classified into different types based on the season of cultivation, habitat conditions and the grain quality.

The Sali type, which comprises majority of rice varieties of the region is cultivated in low-lying flood plains of NE India, mainly in the Brahmaputra and Barak Valley regions. The Boro type is traditionally cultivated during the winter months (November through May) in low-lying areas where sufficient water is available during the cold and dry months of the year. Thus, Boro type rice varieties may contain genotypes suitable for cold adaptation. The dryland cultivated rice varieties, normally grown in slash and burn agriculture system, and locally known as Jum type, show adaptations to a wide range of ecological conditions including low levels of soil moisture in areas at high altitudes reaching over 3000 m above sea level. The glutinous grain type rice is commonly cultivated throughout the region as a source of grain for breakfast and dessert for many ethnic communities in the region. Figure 1.2 shows variation in grain morphology of representative varieties included in this study. In addition to cultivated indigenous rice varieties, natural populations of many wild rice species including $O$. rufipogon, $O$. granulata, O. officinalis, O. nivara, O. meyeriana, Hygrorhizaaristata, Leersiahexandra and Zizenialatifolia are also found in the northeastern region of India (Hore 2005).

The indigenous rice varieties cultivated by traditional farmers may contain a considerable genetic diversity that can serve as a source of germplasm for genetic improvements of cultivated varieties of rice. In general, diverse landraces traditionally cultivated by farmers around the centers of diversity and domestication of crops are


Figure 1.2: Variation in grain morphology of a few representative varieties included in this study. A, Bherapawa; B, Lallatoi; C, Guaroi; D, Joha; E, Hatihali; F, Tilbora.
considered as key natural resources (Pusadee et al. 2009) important for maintaining the future food security in light of the changing climate. Although a few studies have examined the population genetic structure of $O$. sativa germplasm at a global scale (Glaszmann 1987; Garris et al. 2005), region specific studies are limited. Earlier studies based on morphology and agronomic traits (Vairavan et al. 1973; Borkakati et al. 2000; Sarma and Pattanayak 2009) as well as molecular markers (isozyme, RAPD, ISSR) demonstrated a high level of genetic diversity among indigenous rice varieties in NE India (Glaszmann et al. 1989; Sarma and Bahar 2005; Bhuyan et al. 2007). However, these studies were limited either to a particular group of varieties (e.g. glutinous rice and lowland varieties) or to a narrow geographic region. In particular, no extensive studies have focused on the genetic structure of some of the widely cultivated indigenous types such as Boro (cultivated in low-lying perennial water bodies during winter season), Jum (cultivated in upland areas in hill-slopes and low soil moisture condition), Sali (most widely cultivated rice during monsoon season) and glutinous (sticky rice with cultural importance) covering the wider geographic area.

The ongoing rapid changes in agricultural practices that favor agronomically improved varieties has become a serious threat for the persistence of indigenous rice varieties in NE India. Thus, conservation and management strategies are urgently needed to prevent further loss of genetic diversity inherent to indigenous rice varieties in the region. A detailed understanding of the genetic structure and diversity is needed for the planning and implementation of effective conservation, management and utilization of rice germplasm in the whole region.

The objectives of Chapter 1 are to (a) assess genetic diversity among indigenous rice varieties in the Eastern Himalayan region of the NE India, (b) compare the genetic diversity in indigenous varieties with agronomically improved varieties (c) assess distribution of genetic diversity among different types and (d) infer the population genetic structure of rice varieties in NE India.

## Materials and methods

## Plant samples

A total of 29 varieties of cultivated rice (Oryza sativa) were collected from various regions of NE India (Figure 1.1). These samples included 24 indigenous varieties representing Sali (12), Jum (4), Boro (3), and glutinous (5) types and 5 agronomically improved varieties. The variety name, type and locality are given in Table 1.1. Wild rice (O. rufipogon) accessions originally collected from Eastern India were obtained from the International Rice Research Institute (IRRI), Philippines. Either grains or fresh leaf samples were collected from the field and morphological characters were noted based on direct observation or interviewing the farmers. The agronomically improved varieties, released by the regional and central rice research institutes and widely cultivated for their higher yield were obtained from farmers of the region. Seeds were germinated in Petri dishes and transferred to small pots and grown in a greenhouse. Leaf samples from seedlings were harvested, air dried, and used for the study. Genomic DNA was extracted following a modified cetyltrimethyl ammonium bromide extraction protocol (Doyle and Doyle 1987; Dayanandan et. al. 1997).

Table 1.1: Cultivation type, location and genetic diversity values of traditionally cultivated indigenous and agronomically improved rice varieties including the wild rice (O. rufipogon) in northeast India (AP, Arunachal Pradesh; AS, Assam, ML, Meghalaya, MZ, Mizoram)

| Variety Name | Ecotype | Location | A | Na | Npo | Npe | $\mathrm{R}_{\mathrm{A}}$ | $I$ | $H_{\mathrm{e}}$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Lahi | Sali | Doimukh (AP) | 11 | 1.571 | 3 | 42.86 | 1 | 0.271 | 0.187 |
| Local Basmati | Sali | Doimukh (AP) | 9 | 1.286 | 2 | 28.57 | - | 0.148 | 0.105 |
| Borjahinga | Sali | N. Lakhimpur, (AS) | 10 | 1.429 | 2 | 28.57 | - | 0.187 | 0.130 |
| Joha | Sali | Doimukh (AP) | 8 | 1.143 | 1 | 14.29 | - | 0.096 | 0.076 |
| Hati Hali | Sali | N. Lakhimpur, (AS) | 13 | 1.857 | 5 | 71.43 | 1 | 0.377 | 0.263 |
| Balam | Sali | Cachar (AS) | 12 | 1.714 | 3 | 42.86 | - | 0.328 | 0.222 |
| Lallatoi | Sali | Hailakandi (AS) | 23 | 3.286 | 6 | 85.71 | 4 | 0.854 | 0.498 |
| Arfa | Sali | Hailakandi (AS) | 13 | 1.857 | 4 | 57.14 | 1 | 0.438 | 0.305 |
| Mulahail | Sali | Hailakandi (AS) | 20 | 2.857 | 5 | 71.43 | 1 | 0.719 | 0.435 |
| Guaroi | Sali | Hailakandi (AS) | 13 | 1.857 | 5 | 71.43 | - | 0.330 | 0.219 |
| Harinarayan | Sali | Hailakandi (AS) | 11 | 1.571 | 3 | 42.86 | - | 0.262 | 0.166 |
| Bherapawa | Sali | Hailakandi (AS) | 8 | 1.143 | 1 | 14.29 | - | 0.072 | 0.051 |
| Papue | Jum | West Siang (AP) | 9 | 1.286 | 2 | 28.57 | - | 0.143 | 0.105 |
| Sorpuma | Jum | Doimukh (AP) | 10 | 1.429 | 3 | 42.86 | - | 0.239 | 0.181 |
| Kawanglawang | Jum | Aizwal, (MZ) | 17 | 2.429 | 6 | 85.71 | 1 | 0.578 | 0.365 |
| Mimutim | Jum | Garo Hills (ML) | 17 | 2.429 | 5 | 71.43 | 3 | 0.595 | 0.384 |
| Til Bora | Glutinous | N. Lakhimpur, (AS) | 12 | 1.714 | 5 | 71.43 | - | 0.237 | 0.152 |
| Kakiberoin | Glutinous | Hailakandi (AS) | 12 | 1.714 | 4 | 57.14 | - | 0.306 | 0.207 |
| Borua Beroin | Glutinous | Cachar (AS) | 14 | 2.000 | 4 | 57.14 | - | 0.357 | 0.224 |
| Ranga Borah | Glutinous | N. Lakhimpur, (AS) | 13 | 1.857 | 3 | 42.86 | 1 | 0.239 | 0.135 |
| Bas Beroin | Glutinous | Cachar (AS) | 10 | 1.429 | 3 | 42.86 | - | 0.288 | 0.228 |
| Aubalam | Boro | Cachar (AS) | 15 | 2.143 | 5 | 71.43 | 1 | 0.569 | 0.394 |
| Bashful | Boro | Cachar (AS) | 11 | 1.571 | 3 | 42.86 | - | 0.315 | 0.232 |
| Moircha | Boro | Cachar (AS) | 11 | 1.571 | 3 | 42.86 | - | 0.167 | 0.098 |
| Ranjit | Improved | Hailakandi (AS) | 7 | 1 | 0 | 0 | - | 0 | 0.000 |
| IR8 | Improved | Hailakandi (AS) | 7 | 1 | 0 | 0 | - | 0 | 0.000 |
| Bahadur | Improved | Hailakandi (AS) | 7 | 1 | 0 | 0 | - | 0 | 0.000 |
| Pankaj | Improved | Hailakandi (AS) | 7 | 1 | 0 | 0 | - | 0 | 0.000 |
| Joya | Improved | Hailakandi (AS) | 7 | 1 | 0 | 0 | - | 0 | 0.000 |
| O.rufipogon | Wild | Eastern India | 29 | 4.833 | 6 | 85.71 | 4 | 1.137 | 0.556 |
|  |  |  |  |  |  |  |  |  |  |

$\mathrm{A}=$ Observed no. of allele; $\mathrm{Na}=$ Average no. of alleles per 7 loci; $\mathrm{Npo}=\mathrm{No}$. of polymorphic loci; Npe $=$ Percent polymorphic loci; $\mathrm{R}_{\mathrm{A}}=$ Rare allele; $\mathrm{I}=$ Shannon information index; $\mathrm{He}=$ Nei gene diversity.

## PCR assay and genotyping

Seven SSR loci (RM302, RM341, RM130, RM307, RM169, RM204, RM264) with relatively high polymorphism and distributed across the rice genome were selected for the genetic diversity analyses (Table 1.2) (Chen et al. 1997; Temnykh et al. 2000). The forward primers were labeled with IRD700 or IRD800 dye for genotyping in LICOR 4000 IR2 DNA analyzer (Li-Cor Biosciences, Lincoln, NE). The PCR amplifications were performed in $25 \mu \mathrm{~L}$ reaction mixture consisting of 0.2 mM dNTP , $2.5 \mathrm{mM} \mathrm{MgCl}_{2}, 2.5 \mu \mathrm{~L}$ of 10X buffer, 2.5 pmol of each primer and 0.2 U Taq polymerase. The thermocycling profile used was initial denaturation at $94^{\circ}$ ( 3 min ) followed by 35 cycles of $94^{\circ}(2 \mathrm{~min}), 50^{\circ}(1 \mathrm{~min}), 72^{\circ}(2 \mathrm{~min})$ and a final extension of $72^{\circ}$ for 5 min . The amplified products were diluted (1:50) with loading dye (Formamide and Bromophenol blue), denatured at $94^{\circ} \mathrm{C}$ for 5 min and cooled on ice before loading to 6.0\% denaturing polyacrylamide gels on a Li-COR automated DNA sequencer with a size standard (50-350 bp, IRDye700 or IRDye800) (Li-Cor Biosciences).

The size of each amplified fragment was determined by comparison with the size standard and scored to prepare the genotype matrix. To determine the optimum number of individuals per variety to be genotyped to capture the total diversity, the number of individuals analyzed were increased one by one until the number of alleles reached to a maximum with no further increase for a given locus. Figure 1.3 represents the correlation between the number of alleles detected with increasing number of individuals at the SSR locus RM302. Therefore, 300 individuals were genotyped at seven SSR loci for this study. Accordingly, I determined that 10 individuals per variety was sufficient to capture

Table 1.2: Details of SSR loci used in the present study and their genetic diversity parameters.

| Primer <br> name | Chr | SSR motif | Forward 5-3 | Reverse 5-3 | $N \mathrm{Na}$ | $H_{\mathrm{e}}$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| RM302 | 1 | (GT)30(AT)8 | TCATGTCATCTACCATCACAC | ATGGAGAAGATGGAATACTTGC | 10 | 0.805 |
| RM341 | 2 | (CTT)20 | CAAGAAACCTCAATCCGAGC | CTCCTCCCGATCCCAATC | 19 | 0.861 |
| RM130 | 3 | (GA)10 | TGTTGCTTGCCCTCACGCGAAG | GGTCGCGTGCTTGGTTTGGTTC | 4 | 0.419 |
| RM307 | 4 | (AT)14(GT)21 | GTACTACCGACCTACCGTTCAC | CTGCTATGCATGAACTGCTC | 9 | 0.749 |
| RM169 | 5 | (GA)12 | TGGCTGGCTCCGTGGGTAGCTG | TCCCGTTGCCGTTCATCCCTCC | 14 | 0.798 |
| RM204 | 6 | CT)44 | GTGACTGACTTGGTCATAGGG | GCTAGCCATGCTCTCGTACC | 18 | 0.866 |
| RM264 | 8 | (GA)27 | GTTGCGTCCTACTGCTACTTC | GATCCGTGTCGATGATTAGC | 21 | 0.884 |

Chr, Chromosome location; Na , Observed number of alleles; $H_{\mathrm{e}}$, Nei (1973) genetic diversity.


Figure 1.3: Graph showing number of genotyped individuals and corresponding numbers of alleles at the locus RM302.
the total genetic variation in a given variety. Therefore, I genotyped 300 individuals (10 individuals per variety for 30 varieties) at seven SSR loci for the present study.

## Data analysis

The SSR genotype data matrix was used for assessing genetic diversity and structure in a hierarchical manner from overall (all indigenous varieties), through different types, and each variety. The among type genetic diversity was calculated by considering all genotyped individuals of a given type as one population while genetic parameters for among variety was calculated based on 10 genotyped individuals per variety. The observed average number of alleles per locus ( Na ), average allelic richness $\left(R_{\mathrm{S}}\right)$, population differentiation $\left(F_{\mathrm{ST}}\right)$ and Nei gene diversity $(\mathrm{He})$ (Nei 1973) were calculated using FSTAT 2.9.2.3 (Goudet 2001). Allelic richness is the number of alleles for each population averaged over loci and standardized for the smallest population size. Average effective number of alleles $(\mathrm{Ne})$ and Shannon information index ( $I$ ) were calculated using PopGene version 1.31 (Yeh et al. 1999). Average pairwise genetic differences between varieties was calculated using Arlequin 3.5 (Excoffier et al. 2010). Analysis of Molecular Variance (AMOVA) (Excoffier et al. 1992) within variety, among variety and among types was performed in Arlequin 3.5 (Excoffier et al. 2010) to determine the distribution of variation at different hierarchical levels. The statistical significance of the variance components was tested with 1000 permutations.

Genetic distance among varieties were estimated using chord genetic distance method (Cavalli-Sforza and Edwards 1967). The genetic distance based clustering was performed with the unweighted pairgroup method with arithmetic mean (UPGMA) using

PowerMarker v3.25 (Liu and Muse 2005), and the dendrogram was constructed using MEGA software (Kumar et al. 2001). Principal component analysis (PCA) of pairwise genetic distance between individuals was performed using GenALEx v. 6.4 (Peakall and Smouse 2006). The Bayesian model-based clustering analysis was used for determining the optimal number of genetic clusters found among rice varieties using the software STRUCTURE 2.3.3 (Pritchard et al. 2000), which partitions individuals into number of clusters $(K)$ based on the multilocus genotypic data. The admixture model and correlated allele frequencies were applied for each run with 10,000 burn-in period (iteration) and 100,000 Markov Chain Monte Carlo (MCMC) replication. The optimum $K$ value, which indicates the number of genetically distinct clusters in the data, was determined from 10 replicate runs for each value of $K$ (Evanno et al. 2005). The $\Delta K$ was based on the change in the log probability of the data between successive $K$ values. Software program Structure Harvester v6.0 (Earl and von Holdt, 2012) was used for calculating parameters of Evanno et al. (2005). The results of five independent runs were consistently converged to the same values.

## Results

## Overall microsatellite diversity

The seven selected SSR loci amplified DNA fragments from 29 O. sativa varieties and $O$. rufipogon with consistent reproducibility. A total of 96 alleles with an average of 13.57 alleles per locus were detected among all studied samples. The highest number of alleles (21) was detected in the locus RM264 and the lowest (4) was in the locus RM130. The indigenous rice varieties were genetically variable, while
agronomically improved varieties were monomorphic within varieties at all loci. The highest gene diversity value of 0.884 was detected at RM264 and the lowest value of 0.419 detected in RM130 (Table 1.2).

Indigenous rice varieties in NE India showed high level of genetic diversity with an overall allelic richness of 10.205 per locus and a gene diversity value of 0.776 , while the agronomically improved varieties had significantly lower average allelic richness of 2.857 per locus and gene diversity was 0.459 . A very high level of differentiation $\left(F_{\mathrm{ST}}=\right.$ $0.754)$ was also detected among the rice varieties.

## Within variety genetic diversity

The average observed number of alleles among indigenous rice varieties ranged from 1.14 (Joha and Bherapawa) to 3.29 (Lallatoi) while the corresponding value was only 1.00 for the agronomically improved varieties. Some of the elite traditional rice varieties (including Lallatoi, Mulahail, Aubalam, Mimutim) showed very high levels of genetic diversity as measured in average numbers of alleles, rare alleles and Nei gene diversity. Two of these varieties exhibited relatively high numbers of rare alleles $($ Lallatoi $=4 ;$ Mimutim $=3)$. Nei's gene diversity values ranged from 0.051 (Bherapawa) to 0.498 (Lallatoi) with an average of 0.223 across all indigenous varieties. Shannon information content varied widely across varieties from 0.072 (Bherapawa) to 0.854 (Lallatoi) and the average was 0.338 across varieties. The diversity parameters across varieties are presented in Table 1.1. The pairwise genetic differentiation among varieties $\left(F_{\mathrm{ST}}\right)$ ranged from 0.375 to 1.000 and highly significant $(p<0.001)$. The pairwise $F_{\mathrm{ST}}$ values are given in Table 1.3.

Table 1．3：Pairwise $F_{\mathrm{ST}}$ values among different rice varieties of eastern Himalayan region in northeast India and O．rufipogon

|  | $\begin{aligned} & \ddot{\sim} \\ & \frac{\tilde{0}}{0} \end{aligned}$ | $\begin{aligned} & \mathscr{2} \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ |  | 管 | 會. |  |  | $\stackrel{\ddot{2}}{\stackrel{\rightharpoonup}{2}}$ |  |  | $\begin{aligned} & \stackrel{-}{2} \\ & \frac{0}{1} \\ & \stackrel{\rightharpoonup}{2} \\ & 0 . \end{aligned}$ | 恵 | 3 总 弟 | $\begin{aligned} & Q \\ & \stackrel{Q}{0} \\ & 0 . \end{aligned}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Papue | 0.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Sorpuma | 0.634 | 0.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Kawanglawang | 0.703 | 0.581 | 0.000 |  |  |  |  |  |  |  |  |  |  |  |  |
| Mimutim | $0.633$ | $0.690$ | $0.739$ | $0.000$ |  |  |  |  |  |  |  |  |  |  |  |
| Lahi | $0.789$ | $0.691$ | $0.543$ | $0.830$ | $0.000$ |  |  |  |  |  |  |  |  |  |  |
| Local Basmati | 0.834 | $0.726$ | $0.714$ | $0.887$ | $0.831$ | $0.000$ |  |  |  |  |  |  |  |  |  |
| Borjahinga | 0.789 | 0.684 | 0.754 | 0.771 | 0.843 | 0.870 | 0.000 |  |  |  |  |  |  |  |  |
| Joha | $0.742$ | $0.731$ | $0.658$ | $0.867$ | $0.746$ | $0.875$ | $0.884$ | $0.000$ |  |  |  |  |  |  |  |
| Hati Hali | 0.622 | 0.656 | 0.585 | $0.709$ | 0.651 | $0.818$ | 0.763 | $0.663$ | 0.000 |  |  |  |  |  |  |
| Balam | $0.758$ | $0.668$ | $0.713$ | $0.807$ | 0.806 | $0.819$ | $0.797$ | $0.859$ | $0.770$ | $0.000$ |  |  |  |  |  |
| Lal－latoi | 0.594 | 0.519 | 0.582 | 0.655 | 0.674 | 0.610 | 0.566 | 0.720 | 0.603 | 0.598 | 0.000 |  |  |  |  |
| Arfa | $0.724$ | 0.608 | 0.595 | 0.772 | 0.667 | 0.742 | 0.766 | 0.742 | 0.679 | 0.718 | $0.545$ | $0.000$ |  |  |  |
| Mulahail | $0.573$ | 0.529 | 0.542 | $0.564$ | 0.603 | 0.658 | 0.585 | 0.680 | 0.558 | 0.617 | 0.393 | 0.488 | $0.000$ |  |  |
| Guaroi | $0.781$ | $0.657$ | 0.615 | $0.843$ | 0.681 | 0.791 | 0.830 | 0.730 | 0.718 | 0.788 | 0.610 | 0.621 | $0.640$ | $0.000$ |  |
| Harinarayan | $0.837$ | $0.746$ | $0.709$ | $0.880$ | $0.785$ | $0.864$ | $0.859$ | $0.855$ | 0.735 | 0.827 | $0.678$ | $0.739$ | $0.672$ | $0.719$ | $0.000$ |
| Bherapawa | 0.884 | 0.778 | 0.706 | 0.925 | 0.792 | 0.896 | 0.914 | $0.883$ | 0.800 | 0.871 | 0.728 | 0.681 | $0.719$ | $0.737$ | $0.830$ |
| Aubalam | 0.635 | 0.571 | 0.628 | 0.706 | 0.725 | 0.721 | 0.710 | 0.777 | 0.689 | 0.425 | $0.430$ | 0.600 | $0.502$ | 0.703 | 0.740 |
| Bashful | 0.772 | 0.612 | 0.667 | 0.817 | 0.802 | 0.817 | 0.760 | 0.854 | 0.743 | 0.726 | 0.504 | 0.704 | 0.571 | 0.782 | 0.822 |
| Moircha | $0.844$ | $0.743$ | $0.767$ | $0.869$ | $0.863$ | 0.871 | 0.826 | 0.916 | 0.811 | 0.783 | 0.611 | 0.783 | 0.593 | 0.847 | 0.887 |
| Til Bora | $0.698$ | $0.677$ | $0.738$ | $0.802$ | $0.831$ | $0.831$ | $0.804$ | $0.863$ | $0.731$ | $0.789$ | $0.537$ | $0.751$ | $0.652$ | $0.815$ | $0.856$ |
| Kakiberoin | $0.711$ | $0.679$ | $0.674$ | $0.798$ | $0.748$ | $0.797$ | $0.804$ | $0.838$ | $0.704$ | $0.763$ | $0.490$ | $0.698$ | $0.536$ | 0.780 | $0.830$ |
| Borua Beroin | 0.652 | 0.615 | 0.707 | 0.757 | 0.797 | 0.822 | 0.793 | 0.831 | 0.731 | 0.649 | 0.543 | 0.721 | 0.566 | 0.797 | 0.831 |
| Ranga Borah | 0.779 | 0.602 | 0.740 | 0.805 | 0.837 | 0.864 | 0.727 | 0.878 | 0.754 | 0.778 | 0.555 | 0.756 | 0.567 | 0.824 | 0.862 |
| Bas Beroin | $0.724$ | $0.665$ | $0.694$ | $0.741$ | $0.762$ | $0.766$ | $0.757$ | 0.826 | 0.735 | 0.721 | $0.469$ | 0.645 | 0.466 | 0.735 | 0.818 |
| Ranjit | 0.842 | 0.758 | 0.810 | 0.880 | 0.906 | 0.928 | 0.840 | 0.953 | 0.806 | 0.869 | 0.607 | 0.832 | 0.702 | 0.892 | 0.932 |
| IR8 | 0.864 | 0.795 | 0.810 | 0.932 | 0.909 | 0.940 | 0.926 | 0.961 | 0.856 | 0.843 | 0.633 | 0.829 | 0.742 | 0.892 | 0.933 |
| Bahadur | 0.884 | 0.783 | 0.805 | 0.913 | 0.894 | 0.884 | 0.865 | 0.950 | 0.849 | 0.857 | 0.501 | 0.822 | 0.693 | 0.872 | 0.921 |
| Pankaj | $0.780$ | 0.695 | $0.724$ | 0.824 | 0.818 | 0.694 | 0.761 | 0.858 | 0.757 | 0.766 | 0.375 | 0.731 | 0.570 | 0.786 | 0.831 |
| Joya | 0.864 | 0.802 | $0.798$ | 0.915 | 0.896 | 0.935 | 0.900 | 0.958 | 0.838 | 0.853 | 0.641 | 0.826 | 0.588 | 0.895 | 0.935 |
| O．rufipogon | 0.635 | 0.537 | 0.548 | 0.682 | 0.644 | 0.677 | 0.623 | 0.698 | 0.570 | 0.561 | 0.418 | 0.573 | 0.444 | 0.621 | 0.656 |


|  |  |  |  |  | $$ | $\begin{aligned} & \text { H } \\ & \text { O } \\ & \text { O } \\ & \text { O } \end{aligned}$ |  | 0 0 0 0 0 0 0 0 0 |  |  | 䓌: | $\underset{\infty}{\approx}$ |  | $\begin{aligned} & \text { تِ } \\ & \text { 를. } \\ & \text {. } \end{aligned}$ | O |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Papue |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Sorpuma |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Kawanglawang |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Mimutim |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Lahi |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Local Basmati |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Borjahinga |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Joha |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Hati Hali |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Balam |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Lal-latoi |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Arfa |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Mulahail |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Guaroi |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Harinarayan | 0.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Bherapawa | 0.830 | 0.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Aubalam | 0.740 | 0.789 | 0.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Bashful | 0.822 | 0.866 | 0.644 | 0.000 |  |  |  |  |  |  |  |  |  |  |  |  |
| Moircha | 0.887 | 0.929 | 0.720 | 0.739 | 0.000 |  |  |  |  |  |  |  |  |  |  |  |
| Til Bora | 0.856 | 0.901 | 0.639 | 0.779 | 0.830 | 0.000 |  |  |  |  |  |  |  |  |  |  |
| Kakiberoin | 0.830 | 0.848 | 0.645 | 0.750 | 0.824 | 0.743 | 0.000 |  |  |  |  |  |  |  |  |  |
| Borua Beroin | 0.831 | 0.884 | 0.570 | 0.741 | 0.805 | 0.725 | 0.739 | 0.000 |  |  |  |  |  |  |  |  |
| Ranga Borah | 0.862 | 0.909 | 0.682 | 0.715 | 0.808 | 0.793 | 0.796 | 0.782 | 0.000 |  |  |  |  |  |  |  |
| Bas Beroin | 0.818 | 0.846 | 0.619 | 0.727 | 0.749 | 0.749 | 0.657 | 0.741 | 0.736 | 0.000 |  |  |  |  |  |  |
| Ranjit | 0.932 | 0.975 | 0.753 | 0.840 | 0.917 | 0.738 | 0.878 | 0.857 | 0.876 | 0.848 | 0.000 |  |  |  |  |  |
| IR8 | 0.933 | 0.975 | 0.665 | 0.868 | 0.943 | 0.840 | 0.863 | 0.878 | 0.918 | 0.860 | 1.000 | 0.000 |  |  |  |  |
| Bahadur | 0.921 | 0.962 | 0.741 | 0.827 | 0.898 | 0.836 | 0.841 | 0.859 | 0.884 | 0.797 | 0.953 | 0.980 | 0.000 |  |  |  |
| Pankaj | 0.831 | 0.875 | 0.645 | 0.722 | 0.775 | 0.695 | 0.731 | 0.712 | 0.772 | 0.670 | 0.761 | 0.871 | 0.602 | 0.000 |  |  |
| Joya | 0.935 | 0.976 | 0.710 | 0.846 | 0.919 | 0.895 | 0.829 | 0.890 | 0.885 | 0.789 | 1.000 | 1.000 | 0.981 | 0.849 | 0.000 |  |
| O. rufipogon | 0.656 | 0.709 | 0.499 | 0.566 | 0.643 | 0.639 | 0.616 | 0.625 | 0.554 | 0.576 | 0.687 | 0.724 | 0.683 | 0.582 | 0.684 | 0.000 |

Significance level: $p<0.0001$

## Genetic diversity among types

Different levels of genetic variation were observed in different types of indigenous rice from NE India. The highest diversity was detected among the Sali type with an average allelic richness and gene diversity of $7.585( \pm 3.604)$ and $0.747( \pm 0.127)$ respectively. The next level of genetic diversity was detected among the Jum type followed by the glutinous and Boro types (Table 1.4). On the other hand, agronomically improved types showed the lowest levels of diversity (average allelic richness $2.798 \pm 1.438$; average gene diversity $0.459 \pm 0.251$ ). All types showed very high inbreeding coefficient ranging from 0.936 to 1.000 , which could be attributable to the selfing mating system of the cultivated rice. Among indigenous rice varieties, the highest average gene diversity within type $\left(H_{\mathrm{S}(\mathrm{W})}\right)$ was observed in Jum (0.259) and the lowest was in glutinous type (0.189). Population differentiation study within different types showed very low $F_{\mathrm{ST}}$ values ranging from 0.023 in Sali type to 0.036 in Boro type (Table 1.4). The AMOVA results showed statistically significant differentiation ( $\mathrm{p}<0.001$ ) with $25 \%$ variation among individuals, $66 \%$ among varieties and $9 \%$ among cultivation types (Table 1.5).

## Genetic structure analysis

The UPGMA clustering based on chord genetic distance grouped rice varieties into two distinct groups (Figure 1.4). The Group-I in the UPGMA tree consists of both indigenous and the agronomically improved varieties. All agronomically improved varieties clustered within Group-I which could be considered as indica subspecies.

Table 1.4: Population structure and F-statistics of different types of indigenous and agronomically improved rice varieties in NE India

| Type | Allelic <br> richness | Gene <br> diversity | Inbreeding <br> coefficient | $H_{\mathrm{S}(\mathrm{W})}$ | $F_{\mathrm{ST}(\mathrm{W})}$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Sali | 7.585 | 0.747 |  |  |  |
|  | $(3.604)$ | $(0.127)$ | 0.984 | 0.222 | 0.023 |
| Jum | 5.056 |  |  |  |  |
| $(3.061)$ | 0.627 | $(0.187)$ | 1.000 | 0.259 | 0.032 |
|  | 4.727 | 0.602 |  | 0.936 | 0.189 |
| Glutinous | $(1.901)$ | $(0.261)$ <br>  <br> Boro | 3.857 | 0.596 |  |
|  | $(1.864)$ | $(0.280)$ |  |  |  |
| Improved | 2.798 | 0.459 |  |  |  |
| $(1.438)$ | $(0.251)$ | 0.980 | 0.241 | 0.036 |  |
|  |  | 1.000 | 0 | 0.029 |  |

Allelic richness is based on minimum sample size of 30 diploid individuals. $H_{\mathrm{S}(\mathrm{W})}=$ average genetic diversity within type; $F_{\mathrm{ST}(\mathrm{W})}=$ genetic differentiation within type. Values in parenthesis represent standard deviation.

Table 1.5: Analysis of molecular variance (AMOVA) based on 7 SSR loci of traditional and agronomically improved rice varieties in northeast India

| Amova analysis | df | SS | MS | \% of variation | P-value |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Among type | 4 | 294.45 | 129.78 | 8 | $>0.001$ |
| Among varieties | 24 | 912.96 | 76.54 | 66 | $>0.001$ |
| Within varieties | 270 | 366.05 | 2.80 | 26 | $>0.001$ |

df, degree of freedom; SS, sum of square; MS, Means of square.


# Group-II (japonica) 

Figure 1.4: UPGMA tree based on chord genetic distance (Cavalli-Sforza and Edwards 1967) showing genetic relationships among 29 rice varieties in northeast India.

The other group (Group-II) consisted of a few indigenous varieties belonging to Sali and Jum types and could be considered as the japonica subspecies. O. rufipogon accessions appeared intermediate between indica and japonica groups (Figure 1.4). This analysis revealed that $62.5 \%$ of the traditional rice varieties in Eastern Himalayan region of NE India are of subspecies indica while $37.5 \%$ are japonica subspecies.

The UPGMA tree revealed that rice varieties clustered into smaller subgroups based on type, grain quality or geographic origin. For example, Boro, Jum, glutinous, and agronomically improved varieties clustered together into smaller sub-groups within Group-I (indica) while the Group-II (japonica) formed two sub-groups corresponding the geographic locations (Figure 1.5). A few sub-groups and varieties (marked with double asterisk), however, did not cluster with respective types or grain quality (Figure 1.5).

The PCA analysis using pairwise genetic distances revealed that the first three principal components explained $59.91 \%$ of the total variation and showed similar clustering of rice varieties into Group-I (indica) and Group-II (japonica) (Figure 1.6). Three of the agronomically improved varieties (Pankaj, Bahadur and Ranjit) formed a distinct group but showed closer affinity to the Group-I (indica). O. rufipogon accessions showed intermediate position between the two groups (Figure 1.5) similar to clustering in the UPGMA tree.

The Bayesian based analysis of population structure showed that the highest log likelihood is at $K=2$ (Figure 1.7) suggesting two major groups corresponding to two distinct clusters. Individual assignments into two clusters revealed that Group-I (green color, Figure 1.8) consists of $34 \%$ of varieties and include subspecies japonica with


Figure 1.5: Sub-groups of rice varieties within group-I (indica) and group-II (japonica) based on cultivation type, grain characteristics and geographic origin.


Figure 1.6: Principal component analysis of indigenous and agronomically improved rice varieties based on 7 SSR loci. Different varieties grouped together corresponding to two subspecies (indica and japonica).


Figure 1.7: The relationship between $\Delta \mathrm{K}$ and K showing the highest value at $\mathrm{K}=2$.


Figure 1.8: Population structure of traditionally cultivated indigenous and agronomically improved rice varieties in the Eastern Himalayan region. The optimal value of $K=2$.
more than $95 \%$ ancestry. The other $52 \%$ of varieties including agronomically improved accessions formed Group-II (red color, Figure 1.8) corresponding to the subspecies indica with more than $95 \%$ ancestry. However, $14 \%$ of the indigenous varieties showed mixed ancestry of both indica and japonica types.

The comparison of STRUCTURE results with UPGMA and PCA results revealed that three varieties (Kawanglawang, Local Basmati and Bashful; varieties 3, 6, and 18 marked with asterisk; Figure 1.9a) interchanged between Group-I (indica) and Group-II (japonica). However, independent STRUCTURE runs without agronomically improved varieties grouped these varieties into the groups concordant with UPGMA and PCA analyses (Figure 1.9b). Thus, it could be concluded that the results of model based STRUCTURE analysis is in agreement with the UPGMA and PCA based clustering, and grouping of rice varieties is consistent with the classification of indica and japonica types.


Figure 1.9: STRUCTURE output (a) including agronomically improved varieties and (b) without agronomically improved varieties.
Note that three varieties (Kawanglawang, Local Basmati and Bashful; 3, 6, and 18 marked with asterisk) interchanged between groupI (indica) and group-II (japonica) groups (a) while all varieties of group-I (indica) and group-II (japonica) found in UPGMA and PCA analysis clustered together (b)

## Discussion

## Genetic diversity

The present study revealed exceptionally high genetic variation, with an average allelic richness of 10.205 and an overall Nei's gene diversity of 0.776 among indigenous rice varieties in NE India as compared to significantly low average allelic richness (2.798) and gene diversity (0.459) in agronomically improved types. The levels of genetic diversity were also variable across different varieties and much higher than the agronomically improved varieties (Table 1.1). Although the varieties represent only a sub-set of total rice varieties in the region, the gene diversity detected is higher than the overall gene diversity of rice varieties reported from Yunnan province in China (0.706) (Tu et al. 2007) and Indonesia (0.68) (Thomson et al. 2007). The gene diversity detected in my study is comparable to the overall gene diversity of wild rice $O$. rufipogon ( 0.77 ) and $O$. nivara (0.64) populations of the Vientiane Plain of Laos (Kuroda et al. 2007) and the gene diversity of $O$. rufipogon in China ( 0.670 ) (Gao 2004). A previous study based on allozyme markers revealed a moderate genetic variability ( Nei gene diversity $=0.341$ ) among 289 rice varieties from NE India (Glaszmann et al. 1989). The higher gene diversity values detected in the present study could be attributable to high resolving power of microsatellite markers.

The present study revealed several indigenous rice varieties with high genetic diversity, which includes Lallatoi, Mulahail, Aubalam and Mimutim (Table 1.1). Despite the low yield, the traditional farmers in Hailakandi area (Barak Valley region of Assam) have been cultivating Lallatoi, Mulahail and Aubalam for over many generations presumably for its superior nutritional quality and better taste (personal communication).

The local tribal group members in the Garo Hills of Meghalaya pointed out the superior agronomical qualities of Mimutim. Our study revealed high genetic diversity in Mimutum, one of the highly valued rice varieties by native tribal groups. This reflects the importance of traditional knowledge in evaluation and conservation of indigenous crop genetic resources (Brush and Meng 1998).

Most of the indigenous rice varieties are maintained and cultivated by traditional farmers in narrow geographic regions. However, traditional farming practices are in decline due to preference for agronomically improved varieties for higher yield. Therefore, appropriate conservation measures should be taken to promote the cultivation of indigenous varieties with local traditional knowledge.

The genetic diversity maintained in a species is considered as a function of its ecological and evolutionary history (Hamrick and Godt 1996). The high genetic diversity among NE Indian rice varieties have been described in relation to morpho-physiological characters (Vairavan et al. 1973), enzymatic characters (Glaszmann et al. 1989), agromorphological traits (Borkakati et al. 2000) and molecular markers including RAPD (Sarma and Bahar 2005) and ISSR (Bhuyan et al. 2007). The high genetic diversity among rice varieties in the NE Indian region could be attributable to combined effect of wide eco-geographical conditions, diverse agro-ecosystems associated with various rice farming practices and diverse human cultural preferences. High genetic diversity is also reported for other crop plants such as Zingiber officinale (Sajeev et al. 2011), Chilli (Yumnam et al. 2012), Curcuma species (Das et al. 2011), Citrus species (Hazarika 2012) commonly cultivated in NE India, highlighting the importance of the region for germplasm conservation of many crop plants.

I compared the levels of genetic diversity among different types of rice cultivated in NE India, and found that Sali type possessed the highest gene diversity value of 0.747 and average allelic richness of 7.585 . The majority of Sali varieties are maintained by traditional farmers for specific traits such as aroma, grain size and shape, and tolerance to drought, insects and pests, which may contribute to the maintenance of high genetic variation. Jum type also showed high level of heterogeneity with gene diversity of 0.627 and average allelic richness of 5.056. The traditional farming systems and local environment associated with adaptation to diverse conditions including water deficient habitats on the slopes of hilly regions may have contributed to the maintenance of high genetic variability among the Jum type. Due to their inherent high genetic diversity, Sali and Jum types should be prioritized to include in conservation and management plans and future breeding programs.

The high inbreeding coefficient values among rice varieties of the region (Table 1.4) could be due to predominantly selfing breeding system with a very low outcrossing in $O$. sativa species (Oka 1988). The $F_{\text {ST }}$ results (Table 1.4) are also supported by AMOVA (Table 1.5) which indicated that $66 \%$ of the total variation was due to differentiation among varieties. This indicates that rice varieties of the Eastern Himalayan region are highly differentiated.

## Population structure

The UPGMA analyses using genetic distance data clustered rice varieties into two groups, which corresponded to $O$. sativa subspecies indica and japonica (Glaszmann 1987; Oka 1988; Khush 1997). These results agree with the previous isozyme data based
finding that showed the occurrence of two major groups of rice varieties in NE India (Glaszmann 1987). The PCA analysis and Model-based clustering method implemented in the STRUCTURE software also suggested the existence of two major groups corresponding to indica and japonica subspecies. The majority of varieties including agronomically improved rice varieties clustered as one group within the subspecies indica. Most of the varieties were grouped into indica subspecies cluster while few varieties clustered into japonica subspecies. Vairavan et al. (1973) also reported similar results on the basis of amylose content, agronomic, and morphological characteristics. The findings were similar to the study involving Indonesian landraces where $68 \%$ of the varieties were assigned as indica and $32 \%$ as japonica (Thomson et al. 2007). However, a study of European rice collection revealed that $89 \%$ of the accessions belonged to japonica type (Courtois et al. 2012). The O. rufipogon showed intermediate position between indica and japonica types suggesting a possible common ancestry of both indica and japonica types.

Although there was no clear differentiation among Jum, Sali, Boro, and glutinous varieties in the UPGMA and STRUCTURE analysis, the PCA analysis separated the agronomically improved varieties into a distinct group (Figure 1.6) closely associated with the indica type. This is expected as agronomically improved varieties included in the present study were derived from indica type. The STRUCTURE analysis did not show evidence for admixture between the indica and japonica types in almost all varieties. This could be attributable to predominantly selfing or autogamous nature of the breeding system and associated restricted gene flow among populations. Only a few varieties showed mixed ancestry of indica and japonica type (Figure 1.8), which may be either due
to partial differentiation or rare introgression between the two types. Similar structuring reported among Asian cultivated rice Oryza sativa could be due to partial sharing of their ancestral genetic polymorphism and/or recent gene flow (Gao and Innan 2008).

Glaszmann et al. (1989) identified seven groups using isozyme markers and reported typical indica and japonica subspecies, suggesting that varieties mostly grown in mountainous areas of Meghalaya and Arunachal Pradesh belong to japonica. However, the present study revealed that varieties in the mountainous areas of Meghalaya and Arunachal Pradesh represent both japonica and indica types. My results did not correspond to the five major groups described in Garris et al. (2005).

## Conclusion

In summary, high genetic diversity detected among traditional rice varieties in the Eastern Himalayan region of NE India is comparable to genetic diversity detected in wild rice populations in various parts of the world. Several varieties with high genetic diversity and cultural importance were found in Barak Valley region of Assam and Garo Hills of Meghalaya. The Sali and Jum type showed significantly higher levels of genetic diversity compared to agronomically improved types. Rice varieties in NE India clustered into two major groups corresponding to two subspecies, namely indica and japonica. The findings highlights the importance of conservation of rice varieties in NE India as a means of preserving genetic diversity to maintain food security in the changing world.

This chapter is published:
Choudhury, B., Khan, M. L., \& Dayanandan, S. (2013). Genetic structure and diversity of indigenous rice (Oryza sativa) varieties in the Eastern Himalayan region of Northeast India. SpringerPlus, 2(1), 1-10 Highly accessed

## Chapter 2: Genetic Characterization of Indigenous Rice Varieties in the Eastern Himalayan Region of Northeast India


#### Abstract

The Eastern Himalayan region of NE India is home to a large number of indigenous rice varieties, which are traditionally classified as Oryza sativa subspecies indica, japonica or as intermediate types. The traditional method of classification using morphological traits based Cheng index is often inconclusive due to phenotypic plasticity of morphological characters, which are influenced by environmental conditions. In the present study, I used molecular markers specific for indica and japonica subspecies to assess the genetic relatedness of indigenous rice varieties in NE India. The results revealed that the majority of upland cultivated ( Jum ) and glutinous rice varieties, which were traditionally considered as japonica are genetically akin to the subspecies indica. All varieties of Boro ecotype cultivated during winter season were found to be indica type, and only a few lowland and upland cultivated varieties were found to be japonica type. Some of the lowland varieties within the Sali ecotype were intermediate between indica and japonica, and showed a closer affinity to Oryza rufipogon, the wild progenitor of the cultivated Asian rice.


Keywords: Classification, genetic characterization, indel, indica, japonica, Oryza sativa.

## Introduction

The cultivars of Oryza sativa, commonly known as Asian rice are classified into two major groups namely indica and japonica, which are often considered as subspecies based on morphological, physiological and biochemical traits (Oka, 1988; Glaszmann, 1987; Zhang et al. 1992; Yang et al. 1994). The genomic data also support the division of rice cultivars into of two major groups or subspecies of $O$. sativa corresponding to indica and japonica types with relatively distinct genomes that may have originated from a common ancestor about 200,000 to 440,000 years ago (Ma and Bennetzen, 2004; Tang et al. 2004). The traditional classification of indica and japonica subspecies is based on morphological traits combined with physiological and biochemical characteristics. The Cheng index, one of the widely used methods to distinguish these two groups is based on six key characters, namely (1) lemna hairiness, (2) response of rice grains to phenol, (3) inter-node length of panicle axes, (4) color of grain husks, (5) hairiness of leaf-blades, and (6) length to width ratio of grains (Cheng et al. 1984). Based upon Cheng index, cultivars grown in temperate regions (e.g. Japan, Korea and Northern China) are considered exclusively as japonica while the cultivars in tropical and subtropical regions are considered as indica (Zhang, 2009). The rice varieties grown in mountain slopes and high elevations in South and South East Asia are considered as japonica while rice varieties cultivated in the lowland tropical Asia are considered as indica (Oka, 1988; Matsuo et al. 1997). Rice varieties with glutinous or "sticky" grains, which are commonly cultivated in South Asia are also classified as japonica (Oka, 1988).

The rice varieties in NE India are further divided into Sali, Boro and Jum ecotypes based upon the season of cultivation and land-use system. Nursery grown seedlings of the

Sali ecotype are transplanted during the onset of monsoon (Jun-Jul) and harvested during winter (Nov-Dec). The Boro ecotype is cultivated in low-lying areas during the dry winter season (Nov-Dec to Apr-May). The Jum varieties are cultivated on mountain slopes under dry soil conditions. Based on Cheng index, Sali varieties are considered as typical indica whereas few Jum varieties and glutinous grain type varieties are considered as japonica. The majority of the Jum rice varieties in the region are considered as intermediate between indica and japonica types. At present, the Boro ecotype has not been classified into indica or japonica types.

Since the feature of key characters used in Cheng index based classification may vary greatly due to environmental conditions leading to inconclusive distinction between indica and japonica varieties (Lu et al. 2009), molecular marker-based studies are gaining popularity in the characterization of indica-japonica types (Zhang et al. 1992; Long and Xu, 2002; Qi et al. 2009; Zhang et al. 2009). Shen et al. (2004) developed a genome-wide DNA polymorphism database for indica cv 93-11 and japonica cv Nipponbare and identified large number of polymorphic regions including single nucleotide polymorphisms (SNPs) and insertion and deletions (indel) between the genomes of two subspecies. These reflect the gain and loss of a piece of DNA sequence at a particular location of the genome respectively. Indels may vary in size ranging from single nucleotide to several kilobases, and are distributed throughout the genome (Nasu et al. 2002; Feltus et al. 2004). The genotyping based upon indel markers is a relatively simple procedure, which capitalizes on the size difference of the PCR amplification products. Indel markers have been successfully utilized in the identification of rice varieties and in evolutionary studies (Cai et al. 2007; Lu et al. 2009; Liu et al. 2012).

The objectives of the present study were to (i) genetically characterize Sali, Boro, Jum and glutinous rice varieties cultivated in NE India to classify them into indica, japonica or intermediate types and (ii) determine the genetic relatedness among these rice varieties. I hypothesize that the ecotypes genetically similar to indica subspecies may possess more indel markers specific for the indica subspecies and ecotypes closely related to the japonica subspecies may possess more indel markers unique for japonica subspecies. The intermediate varieties may have indel genotypes specific for each variety proportionate to their degree of genetic relatedness to indica or japonica subspecies.

## Materials and methods

## Plant sample

A total of 90 individuals representing 29 rice varieties and one wild rice species were genotyped for 11 markers that discriminate indica and japonica types. These samples included three different ecotypes (Sali, Jum and Boro), which comprised glutinous and nonglutinous grain types and agronomically improved varieties from different parts of NE India (Table 2.1).

Wild rice (O. rufipogon) accessions originally collected from NE India were obtained from the International Rice Research Institute (IRRI), Philippines. Samples of grains or fresh leaves were obtained from farmers in NE India. Morphological characters were noted on the basis of direct observations as well as communications with farmers. Seeds were grown in the green house in small pots and watered regularly. Leaf samples from seedlings were harvested, air-dried and used for the study. Genomic DNA was

Table 2.1: List of rice varieties collected from NE India, their location, cultivation type, (Fi) frequency of indica allele (maximum, minimum and average) and classification using indel marker system (AP, Arunachal Pradesh; AS, Assam, ML, Meghalaya, MZ, Mizoram).

| Variety | Ecotype | Cultivation type | Grain type | $\begin{gathered} F i \\ (\max ) \end{gathered}$ | $\begin{gathered} F i \\ (\mathrm{~min}) \end{gathered}$ | $\begin{gathered} F i \\ \text { (Average) } \end{gathered}$ | Subspecies |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Aubalam | Boro | Lowland | Nonglutinous | 0.91 | 0.91 | 0.91 | Typical indica |
| Bashful | Boro | Lowland | Nonglutinous | 0.91 | 0.91 | 0.91 | Typical indica |
| Moircha | Boro | Lowland | Nonglutinous | 0.91 | 0.91 | 0.91 | Typical indica |
| Borua Beroin | Boro | Lowland | Glutinous | 0.80 | 0.78 | 0.79 | indica |
| Papue | Jum | Upland | Nonglutinous | 0.91 | 0.90 | 0.90 | Typical indica |
| Sorpuma | Jum | Upland | Nonglutinous | 1.00 | 1.00 | 1.00 | Typical indica |
| Kawanglawang | Jum | Upland | Nonglutinous | 0.73 | 0.68 | 0.71 | Close to indica |
| Mimutim | Jum | Upland | Nonglutinous | 0.20 | 0.10 | 0.16 | japonica |
| Lahi | Sali | Lowland | Nonglutinous | 0.09 | 0.09 | 0.09 | japonica |
| Local Basmati | Sali | Lowland | Nonglutinous | 0.91 | 0.90 | 0.90 | Typical indica |
| Borjahinga | Sali | Lowland | Nonglutinous | 0.90 | 0.90 | 0.90 | Typical indica |
| Joha | Sali | Lowland | Nonglutinous | 0.50 | 0.45 | 0.48 | Intermediate |
| Hati Hali | Sali | Lowland | Nonglutinous | 0.50 | 0.50 | 0.50 | Intermediate |
| Balam | Sali | Lowland | Nonglutinous | 1.00 | 0.91 | 0.95 | Typical indica |
| Lallatoi | Sali | Lowland | Nonglutinous | 0.73 | 0.68 | 0.70 | Close to indica |
| Arfa | Sali | Lowland | Nonglutinous | 0.90 | 0.90 | 0.90 | Typical indica |
| Mulahail | Sali | Lowland | Nonglutinous | 0.91 | 0.90 | 0.90 | Typical indica |
| Guaroi | Sali | Lowland | Nonglutinous | 0.55 | 0.55 | 0.55 | Intermediate |
| Harinarayan | Sali | Lowland | Nonglutinous | 0.36 | 0.18 | 0.27 | Close to japonica |
| Bherapawa | Sali | Lowland | Nonglutinous | 0.20 | 0.18 | 0.19 | Japonica |
| Til Bora | Sali | Lowland | Glutinous | 0.90 | 0.89 | 0.90 | Typical indica |
| Kakiberoin | Sali | Lowland | Glutinous | 0.90 | 0.89 | 0.89 | indica |
| Ranga Borah | Sali | Lowland | Glutinous | 0.91 | 0.90 | 0.91 | Typical indica |
| Bas Beroin | Sali | Lowland | Glutinous | 0.96 | 0.91 | 0.93 | Typical indica |
| Ranjit | Sali (Improved) | Lowland | Nonglutinous | 0.91 | 0.89 | 0.90 | Typical indica |
| IR8 | Sali (Improved) | Lowland | Nonglutinous | 0.90 | 0.90 | 0.90 | Typical indica |
| Bahadur | Sali (Improved) | Lowland | Nonglutinous | 0.82 | 0.78 | 0.80 | indica |
| Pankaj | Sali (Improved) | Lowland | Nonglutinous | 0.91 | 0.88 | 0.89 | indica |
| Joya | Sali (Improved) | Lowland | Nonglutinous | 0.80 | 0.78 | 0.79 | indica |
| O. rufipogon | Wild | Lowland | Nonglutinous | 0.56 | 0.42 | 0.47 | Intermediate |

$>0.90=$ Typical indica, 0.75-0.89=indica; 0.61-0.74=close to indica; 0.40-
$0.60=$ intermediate; 0.26-0.39=close to japonica; 0.11-0.25=japonica; $<0.10=$ Typical
japonica.
extracted following a modified cetyltrimethyl ammonium bromide extraction protocol and is given in Chapter 1.

## PCR assay and genotyping

Oligonucleotide primer pairs flanking the Insertion-deletion (indel) sites specific for indica (cv 93-11) and japonica (cv Nipponbare) were selected from available literature (Shen et al. 2004). Eleven indel loci (R1M7, R2M24, R3M23, R4M13, R5M13, R6M30, R7M7, R8M33, R9M20, R10M17, R11M17) distributed throughout the rice genome were selected to genotype the rice varieties including the wild rice, O. rufipogon. The name of the primers, their map positions on the rice genome and annotation is given in Table 2.2. The forward primers were synthesized with a universal M13 tail sequence ( $5^{\prime}$ CACGACGTTGTAAAACGAC) added to the 5 ' end of the oligonucleotide for labeling. The $25 \mu \mathrm{~L}$ PCR reaction mixture contained $0.2 \mathrm{mM} \mathrm{dNTP}, 2.5 \mathrm{mM} \mathrm{MgCl} 2,2.5$ $\mu \mathrm{L}$ of 10X buffer, 2.5 pmol of each primer, 1 pmol of the M13 forward primer labeled with either IRD700 or IRD800, 1 pmol of the reverse primer and 0.2 U of Taq polymerase. Cycling conditions were $94^{\circ}(3 \mathrm{~min})$ followed by 35 cycles of $94^{\circ}(2 \mathrm{~min})$, $50^{\circ}(30 \mathrm{Sec}), 72^{\circ}(2 \mathrm{~min})$ and a final extension of $72^{\circ}$ for 4 min .

The amplified products were diluted (1:5) with loading dye (Formamide and Bromophenol blue), denatured at $94^{\circ} \mathrm{C}$ for 5 min and cooled on ice. The diluted PCR products were loaded on $6.0 \%$ denaturing polyacrylamide gels on a Li-COR 4000 automated DNA sequencer with a size standard (50-350 bp, IRD-700 and IRD-800) (LiCor Biosciences). The migration distance of each allele was compared with the size standard and scored based on the allele sizes. The indel markers were codominant and the

Table 2.2: List of indel markers, their map positions** and annotation in the rice genome.

| Locus | Chr | Position in the genome (indica) | Annotation | Position in the genome (japonica) | Annotation | Indel size (bp) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| R1M7 | 1 | 11647111-11647263 (153) | IGR | 10608641-10608831 (191) | IGR | 38 |
| R2M24 | 2 | 12156089-12156185 (97) | IGR | 11338788-11338915 (128) | IGR | 31 |
| R3M23 | 3 | 17449222-17449415 (194) | ESTR, EST | 15684664-15684818 (155) | UTR (conserved peptide uORF), ESTR, EST | 39 |
| R4M13 | 4 | 107453-107602 (150) | IGR | 8210327-8210495 (169) | IGR | 19 |
| R5M13 | 5 | 6231232-6231438 (207) | IGR | 5992637-5992811 (175) | IGR | 32 |
| R6M30 | 6 | 19409928-19410072 (157) | IGR | 18189560-18189740 (181) | IGR | 24 |
| R7M7 | 7 | 6780445-6780577 (133) | IGR | 6717062-6717261 (200) | IGR | 67 |
| R8M33 | 8 | 22118785-22118914 (130) | IGR | 20794118-20794285 (168) | UTR, ESTR, EST | 38 |
| R9M20 | 9 | 8257287-8257432 (146) | IGR | 9453900-9453994 (95) | IGR | 51 |
| R10M17 | 10 | 7539062-7539244 (183) | Exon (Putative uncharacterized protein), EST | 9088615-9088766 (152) | Exon of gene (LOC_Os10g180 70) EST | 31 |
| R11M17 | 11 | 5437582-5437667 (86) | IGR | 5890341-5890457 (117) | IGR | 31 |

$\mathrm{Chr}=$ Chromosome number; indica $=93-11$; japonica $=$ Nipponbare; values in parenthesis means fragment size (bp);
IGR = Intergenic region on the basis of GRAMENE rice genome database; ESTR = Expressed sequence tag (GRAMENE rice genome database); $\mathrm{EST}=$ Expressed sequence $\operatorname{tag}$ (NCBI database); UTR $=$ Untranslated region.
**on the basis of GRAMENE rice genome database (Release \#32), December 2010, Data recovered on January 20, 2011 (Website: http://www.gramene.org/).
banding patterns were scored as II for homozygous indica, JJ for homozygous japonica and IJ for heterozygous indica-japonica (Lu et al. 2009). The band size (bp) was compared with typical indica (cv 93-11) or typical japonica (cv Nipponbare) cultivars from published literature and the corresponding alleles (II, JJ or IJ) were assigned for each individual. A sample gel image with seven genotyped individuals at three different loci is given in Figure 2.1. In this image, all individuals except individual 2 are homozygous for indica type (hence scored as II) at the locus R6M30 and individual 2 is heterozygous for indica and japonica allele (and hence scored as IJ). Similarly, for the locus R7M7, individuals 2,3, and 4 are homozygous for the japonica allele (JJ); individuals 1,5, and 6 are homozygous for indica allele (II); individual 7 is heterozygous for the indica-japonica allele (IJ); for locus R8M33, individuals 1,3,4 and 6 are homozygous for the indica allele; and individuals 2 and 7 are homozygous for the japonica allele. Average allele frequency of the three genotyped individuals per variety was calculated for accurate identification of the indica and japonica subspecies.

## Data analysis

To characterize a given rice variety as indica or japonica type, I calculated the average indica specific allelic frequency (Fi) of the three genotyped individuals for each variety out of the total number $(\mathrm{N})$ of indel loci examined. The allelic frequency was calculated based on the genotype scores (II, JJ, and IJ) using the formula given in Lu et al. (2009) as follows:


Figure 2.1: Polyacrylamide gel electrophoresis image of 7 rice varieties genotyped with 3 indel markers (R6M30, R7M7, R8M33) showing indica and japonica specific bands.

Frequency of indica alleles $\left(F_{i}\right)=\frac{2 \sum_{1}^{N} X i i+\sum_{1}^{N} X i j}{2 N}$
where, $X_{i i}$ indicates the homozygous indica genotype and $X_{i j}$ indicates the heterozygous indica-japonica genotype at a given indel locus of a particular rice variety; N is the total number of indel loci examined. I calculated the average allele frequency from three genotyped individuals per variety and classified them as typical indica, indica, close to indica (largely as indica) and close to japonica, japonica and typical japonica (largely as japonica). When the frequency of indica alleles for a particular variety is $>0.90$, it is categorized as typical indica type and if the frequency is $<0.10$, the particular variety is characterized as the typical japonica type. The varieties with indica type allele frequencies between 0.40 and 0.60 were classified as intermediate types.

Principal Component Analysis (PCA) was conducted to detect the patterns of genetic differentiation and relationship among the different rice varieties using the software program GenALEx v. 6.4 (Peakall and Smouse, 2006). PCA is a method of detecting patterns of variation in complex data and group individuals based on similarities and dissimilarities to understand the contribution of individuals to the variance of the whole data set. In this analysis, the indel genotype data matrix was used to generate a scatterplot based on the correlation coefficient values and plotted along the different component axes.

To study the genetic structure and relationships among the rice varieties, I applied Bayesian model-based clustering approach using genotype data to determine the optimum number of genetic clusters among the rice varieties using the software STRUCTURE 2.3.3 (Pritchard et al. 2000). The program STRUCTURE divides individuals into a number(s) of clusters ( $K$ ) based on multilocus genotypic data without any prior
population information. The admixture model and correlated allele frequencies were applied for each run with 10,000 burn-in period (iteration) and 100,000 Markov Chain Monte Carlo (MCMC) replication. The optimum $K$ value, which indicates the actual number of clusters in the data, was determined from 10 replicate runs for each value of $K$ (Evanno et al. 2005). The $\Delta K$ was based on the rate of change in the log probability of the data between successive $K$ values.

The indel genotype data were used for calculating Nei's (Nei 1972) genetic distance using the software program PopGene version 1.31 (Yeh et al. 1999). The pairwise distance matrix was used to construct the UPGMA tree using in PHYLIP 3.69 (Felsenstein 2005).

## Results

## Differentiation of indica and japonica

All selected indel loci amplified detectable DNA fragments corresponding to either the indica or japonica type (Figure 2.1). The results indicated that the majority of the rice varieties included in the present study were indica type (typical indica $=52 \%$; indica $=17 \%$; close to indica $=7 \%$ ) while only about $14 \%$ of the varieties were japonica type ( $10 \%$ japonica and $4 \%$ close to japonica). Another $10 \%$ of rice varieties showed intermediate allele frequencies between indica and japonica types. O. rufipogon showed more indica-japonica heterozygous loci than $O$. sativa species and classified as intermediate between indica and japonica type. The genotypic frequency of each type is given in Table 2.1.

Eco-geographically, indica rice is grown primarily throughout tropical Asia at low latitudes and low elevations and japonica types are grown in temperate regions of

East, South East, and South Asia at high latitudes and high elevations (Garris et al. 2005, Cai et al. 2007). Accordingly, all the Sali rice varieties of NE India are generally classified as indica type and all the Jum varieties as japonica type. While the majority of the Sali rice varieties were indica (typical indica, indica or close to indica), about $10 \%$ of the varieties were found to be intermediate type. Interestingly, three out of the four indel marker based japonica type rice varieties belonged to Sali ecotype. These were formerly classified as indica type using Cheng index. Only one out of four Jum varieties (Mimutim) was classified as japonica type using the indel marker system. Glutinous rice varieties, which are traditionally classified as japonica type (Oka, 1988) possessed indel markers typical of indica type. The indel marker based analyses revealed that the Boro ecotype varieties, which are cultivated in limited areas of Assam and its adjoining flood plains in NE India are indica type. The indel markers of all agronomically improved varieties showed affinity to indica type as expected. The wild rice species (O. rufipogon) shared indel markers with both indica and japonica types and classified as intermediate type.

## Genetic structure and relationships

Genetic structure of different rice varieties were assessed using PCA, UPGMA and model based STRUCTURE analysis. The PCA analyses of indica and japonica specific indel genotype data revealed that $51 \%$ and $16 \%$ of the total variance were in the first two axes respectively. Therefore, the PCA should well represent the genetic structure of the different rice ecotypes in NE India. As shown in the Figure 2.2, four japonica varieties (Bherapawa, Harinarayan, Lahi and Mimutim) formed a distinct group at the positive side of the x -axis and the indica types including the agronomically improved varieties


Figure 2.2: The scatter plot of indigenous rice varieties based on principal component analysis (PCA) showing significant genetic differentiation into indica, japonica and intermediate rice genotypes in NE India.
formed a separate group on the negative side of the - axis. Moreover, the intermediate varieties with indel genotypes shared between indica or japonica varieties were scattered between the indica and japonica groups in the centre of the scatter plot along with the wild rice (O. rufipogon).

The STRUCTURE analysis revealed that the highest $\log$ likelihood value at $K=2$, clearly showing genetic differentiation into two major types of rice varieties in the eastern Himalayan region of NE India. Individual assignments into two clusters demonstrated that the first group (Figure 2.3, shown in green) corresponds to the japonica and intermediate types and the second group (shown in red) corresponds to the indica type. Both PCA and STRUCTURE analyses revealed congruent results implying distinct genetic composition corresponding to indica and japonica subspecies. Most of the japonica varieties classified using molecular genetic markers belonged to Sali and glutinous types except for one of the Jum varieties, suggesting a different degree of genetic differentiation among indigenous rice varieties in NE India. Only one intermediate type of variety (Guaroi) did not cluster with the japonica type in the UPGMA tree. Rice varieties of Boro ecotype clustered with indica type in all analyses. On the other hand, three varieties of Sali ecotypes (Joha, Hati Hali and Guaroi) did not show differentiation into indica-japonica types in the PCA method. These varieties also showed admixed ancestry in STRUCTURE analysis. The UPGMA tree based on Nei's (1972) genetic distance values showed that japonica and intermediate type of varieties were clustered together while indica types including all agronomically improved varieties formed a separate group (Figure 2.4).


Figure 2.3: Results of STRUCTURE analysis showing 2 major groups of rice varieties corresponding to indica (red colored segment) and japonica (green colored segment) types. The intermediate varieties with admixed ancestry are indicated in red and green color bars.


Figure 2.4: UPGMA tree based on genetic distance (Nei 1972) among rice varieties.

## Discussion

The traditional classification of $O$. sativa varieties into indica and japonica subspecies based on Cheng index is often inconclusive due to phenotypic plasticity associated with environmental heterogeneity and differential growth conditions. I used indel based molecular markers to distinguish rice varieties of indica, japonica and intermediate types. In addition, the indel genotype data were used for investigating the population genetic structure of representative rice varieties in NE India. The molecular data based on 11 indel loci separated indigenous rice varieties in the Eastern Himalayan region into indica, japonica and intermediate types. The majority of varieties were indica type while few varieties showed japonica type genotypes. A few varieties showed allele frequencies intermediate between the two types indicating genetic admixture of indica and japonica types. Similar results were also reported based on amylose content, agronomic, and morphological characteristics (Vairavan et al. 1973). The wild progenitor of cultivated rice, $O$. rufipogon, showed genotypes intermediate between indica and japonica types as reported earlier (Oka 1988; Sano and Morishima 1992; Xiong et al. 2010). This confirmed the effectiveness of indel marker based classification and the ancestral status of $O$. rufipogon, from which both indica and japonica types may have derived.

In general, rice varieties grown in low latitudes and low elevation areas in tropical Asia are considered as indica type and the varieties grown in temperate East Asia, Southeast Asia, and South Asia at high latitudes and high elevations are considered as japonica type (Matsuo et al. 1997; Garris et al. 2005). However, the present study showed that indica and japonica types cannot be differentiated solely based on altitudinal distribution, cultivation type or grain qualities. For example, Bherapawa, Harinarayan
and Lahi varieties, which are cultivated at low elevation in flood plain areas of Assam showed japonica type genotypes while three of the four Jum varieties (Kawanglawang, Papue and Sorpuma) showed indica type genotypes. Only one Jum variety (Mimutim) possessed genotypes relating it to japonica type. All genetically improved varieties showed indica type genotypes as expected based upon their ancestry, confirming the effectiveness of the indel marker based classification method. On the other hand, three Sali varieties (Guaroi, Hati Hali and Joha) showed intermediate genotypes, which could be attributable to maintenance of either primitive or admixed rice varieties by traditional farmers. The indel molecular marker based classification of wild rice species into intermediate type further demonstrates that both indica and japonica rice types may have evolved from $O$. rufipogon as a progenitor.

The PCA and STRUCTURE analyses supported the pattern of differentiation and genetic divergence of the rice varieties in NE India. The majority of rice varieties included in the present study showed indica characteristics while only a few varieties showed japonica characteristics. This may be explained by the fact that indica rice was domesticated from a broad geographic region of South and South East Asia (Huang et al. 2012) and is still widely cultivated in these areas. The putative ancestral wild rice species, O. rufipogon, showed intermediate type between indica and japonica in PCA analysis and admixed ancestry in STRUCTURE analyses support the idea that both rice subspecies may have evolved from $O$. rufipogon through continuous human selection (Oka, 1988; Khush, 1997; Huang et al. 2012). The UPGMA tree (Figure 2.4) showed that the japonica and intermediate type varieties are genetically more closely related to each other than to the indica type. This suggests a broad genetic differentiation of the indigenous rice varieties in the NE Indian region. Sano and Morishima (1992) also
reported nonrandom association in characters and gametic disequilibrium among the traditional rice varieties in hilly areas of Asia. The resulting information on genetic relatedness of rice varieties is invaluable for choosing rice germplasm for future breeding programs to develop varieties of rice with improved agronomic traits or adaptability to changing climatic conditions.

## Conclusion

The indigenous rice varieties cultivated in the Eastern Himalayan region of NE India are genetically diverse, and comprise predominately indica type with few japonica and intermediate types. In contrary to the traditional view that rice varieties of Sali ecotype are indica type, the indel marker based analyses revealed that some of the Sali varieties are japonica type. Similarly, indel based molecular markers revealed that rice varieties with glutinous grains, which are traditionally classified as japonica type, are genetically akin to indica type. Furthermore, the indel marker based analyses revealed that the Boro rice varieties are indica type. The genetic polymorphism found in intermediate type varieties could be attributable either to the maintenance of ancient polymorphism, or alternatively to recent hybridization and introgression of japonica and indica types. The resulting information on genetic polymorphism and relatedness among indigenous rice varieties in NE India are invaluable for choosing germplasm for breeding programs targeted to improve agronomic traits and adaptability to a variety of climatic conditions.

# CHAPTER 3: Patterns of Nucleotide Diversity and Phenotypes of Two Domestication Related Genes ( $O s C 1$ and $W x$ ) in Indigenous Rice Varieties in 

## Northeast India


#### Abstract

The cultivated crops are a result of plant domestication from their wild progenitors through selection of individuals with specific traits desirable for human needs. Thus, genetic and nucleotide diversity of genes associated with selected traits in crop plants are expected to be lower than their counterparts in the progenitors. In the present study, I surveyed the pattern of nucleotide diversity of two trait specific genes, $W x$ and $O s C 1$, which regulate amylose content and apiculus coloration respectively in cultivated rice varieties. The samples analyzed were collected from a wide geographic area in NE India, and included contrasting phenotypes considered to be associated with selected genes, namely glutinous and nonglutinous and colored and colorless apiculus. The results revealed that mutations of these two genes believed to be associated with specific phenotypes do not necessarily correspond to the phenotypes in indigenous rice varieties in NE India. This suggests that genomic regions other than those previously reported may also be involved determination of these phenotypes. Overall, no statistically significant selection signatures were detected in the sequences. However, of either gene, a low level of selection that varied across the length of each gene was evident. The glutinous type varieties showed higher levels of nucleotide diversity at the $W x$ locus ( $\pi_{\text {tot }}$ $=0.0053)$ than nonglutinous type varieties $\left(\pi_{\mathrm{tot}}=0.0043\right)$. The $O s C 1$ gene revealed low levels of selection among the colorless apiculus varieties with lower nucleotide diversity $\left(\pi_{\mathrm{tot}}=0.0010\right)$ than in the colored apiculus varieties $\left(\pi_{\mathrm{tot}}=0.0023\right)$.


Keywords: Indigenous, Nucleotide diversity, NE India, Rice, Trait specific genes

## Introduction

The domestication of plants and animals, considered as one of the most important events in the human history, increased the food security to support the increasing human population. The process of domestication is complex and involves selection of individuals from wild progenitors to fulfill human needs (Doebley et al. 2006). The Asian cultivated rice is one of the earliest domesticated crop species in the world that was selected for many traits related to human consumption and large-scale agriculture. The most important domestication-related traits and corresponding genes identified so far in rice with significant morphological and physiological modifications include reduction in grain shattering (Konishi et al. 2006; Li et al. 2006a), changes in grain coloration (Sweeney et al. 2006), grain size and shape (Yamanaka et al. 2004), grain fragrance and flavor (Bradbury et al. 2005), grain number (Ashikari et al. 2005), grain weight (Song et al. 2007) and grain stickiness (Yamanaka et al. 2004). The genes that control these traits are often called 'domestication genes' in crop plants. In addition to human mediated selection for specific traits, the environment where crops are grown also may have played a major role in selection and changes in genetic diversity during crop domestication.

Domestication is often associated with reduction in genetic variation in domesticated plants compared to their wild progenitors (Doebley et al. 2006). This is mainly due to population bottlenecks and artificial selection of domestication genes for desirable traits. Domesticated plants are also a product of relatively small founder populations, in which only a sub-sample of the wild progenitor population contributes to the genomes of cultivated plants (Eyre-Walker et al. 1998). As a result, genome-wide loss of genetic variation occurs in cultivated plants (Doebley et al. 2006). The artificial selection targeted to specific desirable traits controlled by domestication genes also
reduces the genetic diversity in crop plants as compared to their wild ancestors (Tanksley \& McCouch 1997). Many traits generally suitable for human needs have been targets of selection during the domestication of crops. These traits and associated genes have subsequently undergone changes due to local environment and cultural preferences (e.g., grain color, taste) (Simmonds 1976). Thus, analyses of nucleotide sequences of domestication genes at the DNA level is invaluable to gain insights into types of selection that has occurred during domestication.

Several studies have demonstrated the selective sweep in domestication genes and genomic regions in domesticated crops (Buckler et al. 2001; Wang et al. 1999). Olsen et al. (2006) showed one to two fold increase in selection pressure in domestication genes compared to genes under strong natural selection. However, the reduction in genetic diversity in different regions within a trait gene may vary depending on the importance of a given region on determining trait.

Indigenous rice varieties cultivated in the Eastern Himalayan region of NE India are phenotypically diverse and many of which are intricately associated with local cultural and traditional practices. One of the most important culinary and cultural practices found throughout NE India is the use of glutinous rice as a food of choice during festival seasons (Roder et al. 1996). Thus, along with nonglutinous rice varieties, numerous glutinous rice varieties are widely cultivated in NE India. The glutinous and nonglutinous nature of rice is primarily determined by the composition of starch in the endosperm tissue. Starch is one of the important components of cereal grains and has been under selection during domestication and subsequent crop diversification (Whitt et al. 2002; Wilson et al. 2004). Starch in rice endosperm contains two types of polysaccharides namely amylose and amylopectin. Rice varieties with high amylose levels ( $\sim 20-30 \%$ )
tend to form discrete, noncohesive (non-sticky) grains when cooked, whereas varieties with lower amylose levels form cohesive (sticky) cooked grains, commonly known as glutinous (Olsen et al. 2006). Previous studies have shown that a mutation in the Waxy ( $W x$ ) gene that encodes granule-bound starch synthase drastically reduces $(<1 \%$ ) synthesis of amylose in the endosperm of glutinous rice (Sano 1984). The point mutation from G to T at the $5^{5}$ splice site of the $W x$ intron 1 is known to cause incomplete posttranscriptional processing of the pre-mRNA in glutinous rice varieties (Sano 1984; Hirano et al. 1998; Isshiki et al. 1998). On the other hand, nonglutinous rice varieties possesses multiple $W x$ alleles and show wide variation in amylose content (Ayres et al. 1997). A highly variable microsatellite $\left(\mathrm{CT}_{\mathrm{n}}\right)$ in the $5^{\prime}$ untranslated exon 1 of the $W x$ gene is known to contain many alleles and the size of the allele is correlated with the amylose content in rice varieties (Ayres et al. 1997; Wan et al. 2007). Some nonglutinous and low-amylose containing varieties also known to carry the G to T mutation at the $5^{\prime}$ splice site of $W x$ gene suggesting that mutation in the $W x$ gene may not necessarily be responsible for the glutinous phenotype (Wang et al. 1995; Cai et al. 1998; Olsen and Purugganan 2002).

Another morphological variation found among indigenous rice varieties in NE India is the apiculus coloration. The wild ancestor of cultivated rice, O. rufipogon, possesses invariant pigmentation in apiculus whereas the apiculus in cultivated rice varieties may be colored or colorless. The colored apiculus phenotype is attributable to anthocyanin pigments, which are known to be associated with coloration in various plant parts. Anthocyanins perform multiple biological functions in plants including protection against UV radiation, defense responses and signal molecules in plant-microbe interactions (Dooner et al. 1991; Koes et al. 1994). Saitoh et al. (2004) identified and mapped the
$O s C l$ gene in rice responsible for anthocyanin pigmentation and apiculus coloration in rice. Comparative sequence analysis revealed that colorless lines differed from their colored counterpart by a 10 bp deletion located in the R 3 repeat within the third exon of the $O s C 1$ gene (Saitoh et al. 2004).

In this study, I explored (a) mutations in $W x$ and $O s C 1$ genes in indigenous rice varieties in NE India, and their corresponding phenotypes, and (b) nucleotide diversity patterns in these genes across rice varieties to discern signature of selection in domestication related genes.

## Materials and methods

## Plant samples

In the present study, altogether 29 cultivated rice varieties (including 5 agronomically improved varieties) and one wild rice species (O. rufipogon) from different parts of NE India were included (Figure 1.1). Two trait specific genes were chosen to study different varieties with contrasting phenotypes. The samples studied included five glutinous and 24 nonglutinous varieties, and 8 colored apiculus and 21 colorless apiculus varieties (Table 3.1). The wild rice species (O. rufipogon), which is nonglutinous and has a colored apiculus was used as an outgroup. Plant morphology and grain characteristics were noted based on direct observation or interviewing the farmers in the field. Protocol for seed germination, seedling growth, leaf harvesting and genomic DNA extraction is given in Chapter 1.

## Loci studied, PCR amplification and sequencing

I analyzed nucleotide polymorphism in two trait specific genes, waxy ( $W x$ ), the gene associated with granule bound starch synthesis and $O s C 1$, the gene associated with anthocyanin biosynthesis and apicule coloration. Nucleotide sequences of oligonucleotide primers used for amplification and sequencing are given in Table 3.2. A portion of the $W x$ gene ( $\sim 2.7-\mathrm{kb}$ region) including the previously identified intron 1 splice donor site mutation, promoter sequence, entire exon 1 , intron 1 , the $5^{\prime}$ end of exon 2 , and the entire noncoding region within exon 2 (Figure 3.1A) were sequenced following the protocol of Olsen and Purugganan (2002). The $O s C 1$ gene region ( $\sim 1.3-\mathrm{kb}$ region) (Figure 3.1B) was amplified and sequenced following Saitoh et al. (2004).

Table 3.1: Rice variety names, phenotype, and functional mutations at the $W x$ and $O s C 1$
gene regions

| Variety | Grain quality | Wx 5' splice site | Wx CTn | Apiculus color | OsC1 10 bp deletion |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Bas Beroin | Glutinous | T | 17 | Colored | No |
| Til Bora | Glutinous | T | 17 | Colored | No |
| Ranga Borah | Glutinous | G | 11 | Colorless | Yes |
| Kakiberoin | Glutinous | G | 11 | Colorless | Yes |
| Borua Beroin | Glutinous | T | 17 | Colorless | No |
| Joha | Non Glutinous | G | 18 | Colored | No |
| Bherapawa | Non Glutinous | G | 17 | Colored | No |
| Lallatoi | Non Glutinous | G | 11 | Colored | Yes |
| Kawanglawang | Non Glutinous | T | 17 | Colored | No |
| Hati Hali | Non Glutinous | G | 18 | Colored | No |
| Balam | Non Glutinous | G | 11 | Colored | No |
| Bashful | Non Glutinous | G | 10 | Colorless | No |
| Lahi | Non Glutinous | G | 17 | Colorless | No |
| Borjahinga | Non Glutinous | G | 11 | Colorless | No |
| Moircha | Non Glutinous | G | 11 | Colorless | Yes |
| Aubalam | Non Glutinous | G | 11 | Colorless | Yes |
| Papue | Non Glutinous | G | 20 | Colorless | Yes |
| Sorpuma | Non Glutinous | G | 10 | Colorless | Yes |
| Mimutim | Non Glutinous | G | 18 | Colorless | Yes |
| Local Basmati | Non Glutinous | G | 11 | Colorless | Yes |
| Arfa | Non Glutinous | G | 11 | Colorless | Yes |
| Mulahail | Non Glutinous | G | 10 | Colorless | Yes |
| Guaroi | Non Glutinous | G | 17 | Colorless | Yes |
| Harinarayan | Non Glutinous | G | 17 | Colorless | Yes |
| Ranjit | Non Glutinous | G | 11 | Colorless | Yes |
| IR8 | Non Glutinous | G | 11 | Colorless | Yes |
| Bahadur | Non Glutinous | G | 11 | Colorless | Yes |
| Pankaj | Non Glutinous | G | 12 | Colorless | Yes |
| Joya | Non Glutinous | G | 11 | Colorless | Yes |
| O. rufipogon | Non Glutinous | G | 7 | Colored | No |

Abbreviations: Wx, Waxy gene; CTn, number of CT repeats

Table 3.2: List of genes surveyed and primer sequences used in the study

| Gene Name | Primer name | Primer sequence ( $5^{\prime}-3^{\prime}$ ) | Functional association |
| :---: | :---: | :---: | :---: |
| Waxy (Olsen and Purugganan 2002) | WxU1F | GCCGAGGGACCTAATCTGC | Granule-bound starch synthase |
|  | Wx1R | TGGTGTGGGTGGCTATTTGTAG |  |
|  | Wx2FaF | GCCCCGCATGTCATCGTC |  |
|  | Wx2R | GTTGTCTAGCTGTTGCTGTGGA |  |
|  | Wx1Fint | TTGTCAGCACGTACAAGCA |  |
|  | Wx2Rint | GCTATATACATTTTCCTTTGACCAA |  |
| OsC1 (Saitoh et al. 2004) | OsC1F1 | ATCGCTCAGTCTCACACCGCA | Anthocyanin biosynthesis |
|  | OsC1F3 | GAGGGA GAATGGGGAGGAGAGC |  |
|  | OsCF4 | TAATTGTGATCTGTATGGATGCTG |  |
|  | OsC1F5 | GATCGATCGTGTATATATGTTGTCAGGT |  |
|  | OsC1R6 | GTTGCTGTGTCGGTGT CGGCG |  |
|  | OsC1R7 | ATGGCCGTCTCCTAATTCCCCTGC |  |
|  | OsC1R2 | CGTACGGACGACGAACTAATGTCAC |  |



Figure 3.1: The locations of the coding and non-coding regions of $W x$ (A) and $O s C 1$ (B) genes. Arrows at the bottom indicate primers used for PCR amplification.

PCR amplifications were performed in an Applied Biosystems thermal cycler in a total volume of $25 \mu \mathrm{~L}$ reaction mixture consisting of $0.25 \mathrm{mM} \mathrm{dNTP}, 2.0 \mathrm{mM} \mathrm{MgCl} 2,2.5$ $\mu \mathrm{L}$ of 10X buffer, 1.5 pmol of each primer and 0.2 U Taq polymerase. The thermal cycling profiles as described in previous publications ( $W x$ : Olsen and Purugganan 2002, and $O s C 1$ : Saitoh et al. 2004) were followed. The amplified DNA products were separated through electrophoresis on $1 \%$ agarose gels containing with $0.33 \mu \mathrm{~g} / \mathrm{ml}$ ethidium bromide. The electrophoresis was performed at 90 V for 40 minutes in a 24 cm long electrophoretic apparatus containing $1 \mathrm{X} \mathrm{TBE} \mathrm{electrode} \mathrm{buffer}$. agarose gels were visualized using an ultraviolet (302 nm) transilluminator (UVP Inc), and the size of the amplified DNA fragments was determined using GeneRuler 1kb DNA ladder (Fermentas) as a size standard. The PCR products were either directly sequenced or sequenced after purification using Bio-Basic PCR product purification kit (Bio-Basic inc.). DNA sequences of the two genes ( $W x$ and $O s C 1$ ) obtained for this study are given in appendix 1 and 2.

## Data analysis

DNA sequence chromatograms were analyzed using the software program Geneious version 5.4.6 (http://www.geneious.com/) and visually inspected for any ambiguities. The resulting consensus DNA sequences were aligned using the software program ClustalW v2 (Larkin et al. 2007). The coding and non-coding regions of the gene were identified by comparison with annotated DNA sequences of corresponding genes downloaded from the genbank.

In order to examine the patterns of nucleotide diversity resulting from evolutionary changes in DNA sequences in relation to neutral expectations and signatures of selection during the domestication process, several analyses as described below were performed using the software program DnaSP version 5.1 (Librado and Rozas 2009). The $\theta_{\mathrm{w}}$ based on the number of segregating sites (Watterson 1975), $\pi$ based on mean pairwise nucleotide differences among sequences (Nei, 1987), Tajima's $D$ (Tajima 1989), Fu and Li's $D^{*}$ and $F^{*}$ (Fu and Li 1993) were calculated, and McDonald and Kreitman (1991) analysis was performed. $D^{*}$ and $F^{*}$ are more sensitive than Tajima's $D$ in detecting deviations from neutrality based on low-frequency polymorphisms, population expansion and positive selection (Fu and Li 1993). The McDonald Kreitman (1991) test is insensitive to demographic histories and geographic structuring of the populations. Thus, use of a variety of approaches that differ in underlying assumptions provides a means to discern the historical processes associated with shaping the patterns of nucleotide diversity. The changes in nucleotide diversity and associated statistic in different regions of the gene was examined using the sliding-window analysis approach. The rates of synonymous ( $d S$ ) and non-synonymous ( $d N$ ) substitution in each of the selected genes among different rice types were calculated. The ratio of $d N / d S$ provides an insight into the long-term selective pressure and purifying selection during the domestication process.

## Results

A total of 53 indel polymorphisms with an average length of 3.525 were detected from the two sequenced regions (Table 3.3). The size of indels varied in length and ranged from one to 20 nucleotides and distributed along both coding and noncoding regions. Single nucleotide polymorphisms (SNP) were more frequent than indels. Total numbers of SNPs found among the sequenced regions were 91 with an average of 1 SNP at every 44.33 nucleotides.

## Polymorphism of the Wx gene

The aligned length, including both coding and non-coding regions of the $W x$ gene was 2770 nucleotides. A total of 50 indels were detected with an average length of 2.12 nucleotides across all samples. The exon 1 (5' untranslated region) of the $W x$ gene contained a highly variable microsatellites $\left(\mathrm{CT}_{\mathrm{n}}\right)$. A total of seven alleles of this microsatellite $(\mathrm{n}=7,10,11,12,17,18$, and 20) were detected among rice varieties included in the present study. Alleles $\mathrm{CT}_{10}, \mathrm{CT}_{11}, \mathrm{CT}_{17}$, and $\mathrm{CT}_{18}$ were found in $3,13,8$ and 3 cultivated varieties respectively. The $\mathrm{CT}_{12}$ and $\mathrm{CT}_{20}$ alleles were found in one cultivated variety each. A unique $\mathrm{CT}_{7}$ allele was found in the wild rice $O$. rufipogon. The number of SNPs was higher than the number of indels, with a total of 84 SNPs resulting in average 1 SNP for 32.98 bp among all samples. Relatively fewer SNP (1) and indels (6) were found in glutinous varieties than in the nonglutinous varieties (17 indels and 7 SNPs). The total number of mutations was also higher among the nonglutinous varieties than in the glutinous varieties (Table 3.4).

The G to T mutation at the $5^{\prime}$ splice donor site of the $W x$ intron 1, which is known to be associated with drastic reduction in amylose synthesis in glutinous rice varieties

Table 3.3: Lengths of aligned gene regions (bp) and site categories

| Gene <br> region | Total <br> length <br> including <br> indels | Total no. of <br> sites <br> excluding <br> indels | No. of <br> indels <br> sites | No. of indel <br> polymorphisms | Length of <br> coding region <br> excluding <br> indels | Length of coding <br> region including <br> indels | Length of <br> noncoding <br> region excluding <br> indels | Length of <br> noncoding <br> region including <br> indels |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Waxy | 2770 | 2574 | 195 | 50 | 177 | 197 | SNP |  |  |
| OsC1 | 1296 | 1284 | 12 | 3 | 809 | 824 | 2593 | 874 | 476 |

(Sano 1984) was not consistently present among glutinous rice varieties included in the present study. The results revealed that T nucleotide was present in four varieties, while G nucleotide was found in the remaining 25 cultivated rice varieties and in the wild rice. The T nucleotide was found in three of the five glutinous varieties (Borua Beroin, Bas Beroin and Til Bora), and G nucleotide was present in other two glutinous (Ranga Borah and Kakiberoin) varieties. On the contrary, the T nucleotide at this site was found in one of the nonglutinous (Kawanglawang) varieties.

The nucleotide diversity analyses results showed that nucleotide diversity of glutinous varieties was higher ( $\pi_{\text {tot }}=0.0053 ; \theta_{\text {tot }}=0.0043$ ) than the nonglutinous varieties $\left(\pi_{\text {tot }}=0.0043 ; \theta_{\text {tot }}=0.0033\right)$. The sliding window analysis of the $W x$ gene revealed high nucleotide diversity at three regions located at 1 to 600,1150 to 2000 and 2300 to 2500 bp of the gene. This analysis further revealed that polymorphic sites were mostly located at the beginning and end of the promoter region, the exon 1 carrying the microsatellite and the first part of intron 1 (Figure 3.2).

## Neutrality analysis at the Wx locus

The estimates of Tajima's $D$ and Fu and Li's $D^{*}$ and $F^{*}$ showed positive values for glutinous and nonglutinous varieties at the $W x$ locus (Table 3.4), indicating overdominant selection or population size reduction. The sliding window analyses of Tajima's $D$ showed that glutinous varieties had only positive values while nonglutinous varieties had both positive and negative values at different regions of the gene (Figure 3.3). Negative $D$ values were detected in the regions between 1357-1432, 1575-1655, 2400-2476, 2659-2735 bp only in nonglutinous varieties. These regions are located in the


Figure 3．2：Nei＇s Nucleotide diversity $(\pi)$ patterns along $W x$ gene（promoter region； exon；intron）in sliding window among glutinous and nonglutinous grain types．Analysis was performed using a window length of 50 bp and steps of 25 bp
（ $\square$ promoter region；皿 exon；$[$ intron）．


Figure 3．3：Tajima＇s $D$ statistics in sliding window analysis for the $W x$ locus among glutinous and nonglutinous rice varieties．Computation was performed using a window length of 50 bp and steps of 25 bp （皿 promoter；$\square$ exon；胃 intron）．

Table 3.4: Levels of nucleotide variation at the two studied gene regions

| Gene | Ecotype | Indel | SNP | S | $\pi_{\text {tot }}$ | $\theta_{\text {tot }}$ | $\mathrm{dN} / \mathrm{dS}$ | $D$ | $D^{*}$ | $F^{*}$ |
| :---: | :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $W x$ | Glutinous | 6 | 1 | 23 | 0.0053 | 0.0043 | - | 1.7295 | 1.7295 | 1.8583 |
|  | Nonglutinous | 17 | 7 | 31 | 0.0043 | 0.0033 |  | 1.1825 | 0.9145 | 1.369 |
| $O s C 1$ | Colored | 2 | 1 | 6 | 0.0023 | 0.0020 | - | 0.8109 | 1.0088 | 1.1449 |
|  | Colorless | 3 | 8 | 10 | 0.0010 | 0.0021 | 1.00 | -1.7683 | -1.2847 | -1.7178 |

S, number of segregating sites; $\pi$, average number of nucleotide differences per site between two sequences (Nei 1987) calculated on the total number of polymorphic sites $\left(\pi_{\text {tot }}\right)$; silent sites $\left(\pi_{\text {sil }}\right)$; synonymous sites $\left(\pi_{\text {syn }}\right)$; nonsynonymous sites $\left(\pi_{\text {nonsyn }}\right)$; $\theta$, Watterson's estimator of nucleotide polymorphism per base pair (Watterson 1975) calculated on the total number of segregating sites $\left(\theta_{\text {tot }}\right)$; silent sites $\left(\theta_{\text {sil }}\right)$; synonymous sites $\left(\theta_{\text {syn }}\right)$; nonsynonymous sites $\left(\theta_{\text {nonsyn }}\right)$; D, Tajima's $D$ (Tajima 1989); $D^{*}$, Fu and Li's $D^{*} ; F^{*}$, Fu and Li’s $F^{*}$ (Fu and Li 1993).
§Tajima's $D$, *Fu and Li's $D^{*}$ and $F^{*}$ not significant ( $\mathrm{P}>0.10$ ).
intron-1 and 2 and the exon-1 of the $W x$ gene. However, the values of $D$ or $D^{*}$ and $F^{*}$ did not differ significantly from zero. Therefore, the observed pattern of variability is not significantly different from expected variability under the neutral model of evolution and neutrality hypothesis cannot be rejected. The McDonald and Kreitman test did not show departure from neutrality for the glutinous and non-glutinous varieties (Table 3.5) indicating no signature of positive selection at the $W x$ locus.

## Polymorphism at the OsC1 gene

The aligned $O s C 1$ gene region was 1296 bp long and included both exons and introns. The results of the present study showed that $62 \%$ of the sequenced samples contained the 10 bp deletion in the R 3 repeat region of the OsCl gene known to cause a frameshift leading to colorless apiculus in rice (Saitoh et al. 2004). In congruent with the expected phenotype of the genotype, the 10 bp deletion was found in 17 colorless apiculus varieties included in the present study and the corresponding deletion was absent in seven colored apiculus varieties and $O$. rufipogon (Table 3.1). However, there were incongruences between the genotype and the phenotype of several varieties examined in the present study. The 10 bp deletion was not found in four colorless apiculus varieties (Bashful, Borua Beroin, Lahi and Borjahinga), and the corresponding 10 bp deletion was found in one of the colored apiculus varieties (Lallatoi).

Three non-synonymous substitutions were detected in the coding regions of the OsC1 gene. One single nucleotide polymorphism (SNP) was detected in the exon-1 with a mutation of G to C at the position 60 resulting in an amino acid change from positively charged Lysine to negatively charged Aspartic acid. Another SNP was detected in the
exon-1 with a mutation of C to G at the position 122 in the variety Bashful, resulting in an amino acid change of non-polar Proline to positively charged Arginine. The other nonsynonymous substitution was at the position 845 in the exon 3 with a mutation of G to T resulting in an amino acid change of Alanine to Valine (both hydrophobic). Other than these, eight SNPs were detected in the intronic regions of the $O s C 1$ gene among different cultivated varieties and wild rice.

The analyses of nucleotide sequences of the $O s C 1$ gene revealed three indels (average 3.22 bp long) and seven SNPs (average one SNP for every 185.14 bp ) among sequenced samples. More indels and SNPs were found in colorless apiculus varieties than in the colored apiculus varieties (Table 3.4). However, the nucleotide diversity ( $\pi$ : Nei 1987) was higher in the colored apiculus rice varieties than in the colorless apiculus varieties (Table 3.4). The sliding window analysis of the $O s C 1$ gene showed that parts of the intron 2 and exon 3 at 400 to 625,800 to 900 and 1050 to 1250 bp are polymorphic, and the nucleotide diversity in colored apiculus varieties are higher than the colorless apiculus rice varieties (Figure 3.4).

## Neutrality analysis

The overall values of Tajima's $D$ and Fu and Li's $D^{*}$ and $F^{*}$ were negative in colorless apiculus rice varieties, and positive in colored apiculus varieties (Table 3.4). The sliding window analyses of Tajima's $D$ showed mostly negative values in colorless apiculus varieties and mostly positive values in the colored apiculus rice varieties (Figure 3.5). The negative D values in colorless apiculus varieties were detected at 25-150, 400475, 525-700, 811-886 and 1161-1237 bp positions a positive value was observed at 475-

525 bp position. On the contrary, colored apiculus varieties showed positive $D$ values in most regions (400-475, 525-625, 811-886 and 1161-1237 bp) and negative values at the 475-525 bp region (Figure 3.5). In general, the colorless apiculus varieties showed negative D values in the exon- 1 , intron- 2 and exon- 3 , and positive D value in the intron2. Interestingly, an opposite trend was observed in colored apiculus varieties with positive $D$ values in intron-2 and exon- 2 and negative $D$ in value in intron- 2 . However, the D values were not significantly different from zero, and therefore neutrality hypothesis cannot be rejected. The McDonald and Kreitman test did not show evidence of selection in the OsCl gene (Table 3.5).


Figure 3.4: Nei's Nucleotide diversity ( $\pi$ ) patterns along $O s C 1$ gene in sliding window among red and colorless colored apiculus in rice. Analysis was performed using a window length of 50 bp and steps of 25 bp . ( exon; intron).


Figure 3.5: Tajima's D statistics in sliding window analysis for the $O s C 1$ locus among the colored and colorless apiculus rice grains. Computation was performed using a window length of 50 bp and steps of 25 bp . ( $\square$ exon; $\mathrm{Q}_{\mathrm{d}}$ intron).

Table 3.5: McDonald-Kreitman test for the $W x$ and $O s C 1$ genes between different types and $O$. rufipogon

| Locus | Ecotypes and <br> grain qualities | Silent |  | Non Synonymous |  |
| :--- | :--- | :---: | :---: | :---: | :---: |
|  | ara Fixed | Polymorphic | Fixed | Polymorphic |  |
| $W x$ | Glutinous | 80 | 22 | 2 | 2 |
|  | Nonglutinous | 80 | 25 | 2 | 3 |
| OsCl | Red apiculus | 3 | 6 | 1 | 0 |
|  | Colorless apiculus | 3 | 8 | 1 | 2 |

${ }^{a}$ Fixed differences in comparison with $O$. rufipogon.

## Discussion

The present study reports the findings of the analyses of DNA sequence variability of two trait specific genes in indigenous rice varieties in the Eastern Himalayan region of NE India. The $W x$ gene is associated with amylose synthesis, which determines the glutinous or nonglutinous nature of rice grains. The OsC1 gene is involved in the synthesis of anthocyanin and associated with coloration of the apiculus in rice grains. The rice varieties used in this study include glutinous and nonglutinous as well as colored and colorless apiculus types collected from a broad geographic area covering most of the NE India.

The present study revealed that previously identified mutations do not exclusively contribute to the corresponding phenotypes in rice varieties. For example, the glutinous nature in most rice varieties is considered to be a result of a G to T mutation at the $5^{\prime}$ splice donor site of exon 2 of the Wx gene (Wang et al. 1995; Hirano et al. 1998). In the present study, three of the five glutinous varieties carried the G to T mutation at the $W x$ gene, while this mutation was not detected in two of the five glutinous rice varieties. On the other hand, one of the 25 non-glutinous rice varieties carried the G to T mutation, while maintaining the non-glutinous phenotypes. This finding suggests that alternative genes or genomic regions other than the ones previously reported are associated with the glutinous and nonglutinous phenotype of the cultivated rice. Similarly, several reports indicated a correlation between variation in amylose content and the number of repeats in the microsatellite region within the Wx gene (Shu et al. 1999; Bao et al. 2006). Although the present study also reports the occurrence of highly variable microsatellite locus within
the $W x$ gene, there was no direct correlation between the number of repeats and the glutinous nature of rice grains.

Analyses of the $O s C 1$ locus also revealed similar patterns. The colorless apiculus in rice varieties is often ascribed to a 10 bp deletion in the OsCl gene (Saitoh et al. 2004). Although 17 of 21 varieties with colorless apiculus included in the present study were associated with the 10 bp deletion in the $O s C 1$ gene, five varieties without the corresponding 10 bp deletion showed the colorless phenotype. Similarly, eight varieties without the 10 bp deletion showed colored apiculus phenotype as expected, whereas one of the varieties with the 10 bp deletion showed the colored apiculus phenotype. Thus, apiculus color phenotype of $18 \%$ of indigenous rice varieties in NE India did not correspond with the reported apiculus color determining genotype of the $O s C 1$ gene.

One of the varieties with colorless apiculus phenotype (Mimutim) had the 10bp deletion in the R 3 region, however, showed the G to C nucleotide change resulting a substitution from Lysine to Aspartic acid and could have suppressed the phenotype. Another colorless apiculus variety (Bashful) without the 10 bp deletion showed an amino acid change from Proline to Arginine in exon-1 suggests that this mutation could be associated with the coloration of the apiculus. However, the other three colorless apiculus varieties (Borua Beroin, Lahi and Borjahinga), which lack the 10 bp deletion in exon-3, did not carry the Proline to Arginine amino acid change suggesting that other genomic regions also play a role in determination of the phenotype of the apiculus color. The mutation at the position 845 of the exon- 3 , which substitutes Alanine to Valine in three varieties and (Tilbora, Kawanglawang and Balam) and O. rufipogon showed no effect on the phenotype of the apiculus color, suggesting that the substitution of an amino acid with
similar hydrophobicity at this position does not affect the apiculus color phenotype. Overall, these observations suggest that multiple genomic regions are involved in determining a particular phenotype. There are several examples of involvement of multiple genes or interacting loci in determination of the phenotype have been reported (Doebley et al. 1990; Olsen and Purugganan 2002, Zhu et al. 2012). Two of the SNPs, C to $G$ mutation at position 122 in exon 1 and $G$ to $T$ mutation at position 845 , had been previously identified (Saitoh et al. 2004). However, the mutation $G$ to $C$ at position 60 in exon 1 is reported for the first time in this study.

It is well known that the domestication process reduces the nucleotide diversity at domestication related genes that control specific traits selected during the domestication. In other words, genes that regulate particular trait under positive selection during domestication and improvement process may imprint 'signatures of selection' in the form of typical patterns of reduced nucleotide diversity (Tanksley and McCouch 1997). This is evidenced by much lower levels of nucleotide diversity among glutinous rice at the $W x$ gene as compared to the nonglutinous rice varieties (Olsen and Purugganan 2002; WeiHua et al. 2012). Similar observations of significantly reduced levels of nucleotide sequence polymorphism in the nonshattering $\operatorname{sh} 4$ allele in the cultivated rice varieties as compared to wild progenitors (Zhang et al. 2009), and reduced diversity in the ramosal gene in cultivated maize as compared to the wild teosintes that control branching architecture in the tassel and ear (Sigmon and Vollbrecht 2010) have been reported. However, the present study revealed higher levels of nucleotide diversity ( $\pi_{\mathrm{tot}}=0.0053$ ) in the glutinous type varieties than in the nonglutinous type varieties $\left(\pi_{\text {tot }}=0.0043\right)$ at the $W x$ locus. This could be attributable to the fact that $W x$ gene, which has been associated
with the glutinous nature of rice, may not be the sole gene that determines the glutinous phenotype. This phenotype is likely controlled by multiple loci which is further evidenced by the fact that the $W x$ intron 1 splice donor site mutation (G to T ) is also found in some nonglutinous rice varieties reflecting that this mutation is not necessarily responsible for the expression of glutinous phenotype (Inukai et al. 2000; Yamanaka et al. 2004). Although selective sweeps may drastically reduce nucleotide diversity in target genes such as $W x$ locus (Olsen et al. 2006), the diversifying selection due to environmental heterogeneity and local cultural preferences may increase nucleotide diversity (Mikami et al. 2008). The existence of diverse agroclimatic conditions, and various cultural traditions of indigenous communities may have played a significant role in the maintenance of high levels of diversity in glutinous varieties of rice in NE India.

In the present study, positive values of Tajima D values were detected for the glutinous and non-glutinous varieties (Table 3.4) except for small regions of the $W x$ gene that showed negative values among nonglutinous varieties (Figure 3.3). Since the values of Tajima's $D$ were not significantly different from zero, the overall distribution of nucleotide diversity falls within the neutral expectations (Table 3.4), and variability of Tajima D values could be considered only as general trends. Since demographic changes including population expansion or reduction may influence all regions of the genome equally, the differences in Tajima D within and between loci could be attributable to selection trends during the domestication process. Therefore, regions of the gene that show positive Tajima D values could be attributable to balancing or overdominant selection, whereas the regions of the gene with negative Tajima D value could be associated with the purifying selection. Signature of positive selection shown in the

McDonald and Kreitman test at the $W x$ gene may be linked to some traits of ecological adaptation into diverse agroclimatic conditions.

The $O s C 1$ gene showed lower levels of polymorphism and reduced nucleotide diversity among the colorless apiculus varieties as compared to colored apiculus varieties. The low level of nucleotide diversity is common in genes related to selected phenotypes (Olsen and Purugganan, 2002; Zhang et al. 2009). Sliding window analysis of the nucleotide diversity showed that most regions of reduced nucleotide diversity in $\mathrm{OsC1}$ gene were same between colored and colorless apiculus phenotypes (Figure 3.4). Such concordant loss of diversity could be attributable to population bottleneck during the domestication (Liu and Burke, 2006).

The evidence for selection among colorless apiculus varieties is detected through high $\mathrm{dN} / \mathrm{dS}$ ratio at the $O s C 1$ locus (Table 3.4). As the gene is associated with synthesis of anthocyanins, which have multiple functions including plant defense responses and signal molecules in plant-microbe interactions (Dooner et al. 1991; Koes et al. 1994), selection of the gene among the cultivated rice varieties can not be ruled out. The negative values of the Tajima $D$ values indicate an excess of rare alleles (Table 3.4) at the OsC1 locus among the colorless apiculus varieties suggesting a possibility of purifying selection. In the present study, it has been found that colorless apiculus varieties possessed more negative $D$ values in the coding regions compared to the colored apiculus counterpart. These patterns are consistent with a recent selective sweep at the OsCl gene among the colorless apiculus rice varieties. Translation of the coding regions of OsC1 gene revealed that the sequences having the 10 bp deletion within the third exon drastically reduces the protein size from 272 amino acids to 206 amino acids. This might
have significant impact in expression of the $O s C l$ gene and regulation of apiculus coloration in rice.

## Conclusion

The present study based on two trait specific genes, $W x$ and $O s C 1$ reported to be associated with amylose content and apiculus coloration respectively, showed that mutations considered to be associated with a given phenotype of the trait do not necessarily correspond to the phenotypes in indigenous rice varieties of NE India. This suggests that alternative genomic regions are also involved in controlling the amylose content and apiculus coloration in rice. Although statistically significant signatures of selection were not detected in either genes, low level of selection that varied across the length of each gene was evident.

## General Conclusion

Indigenous rice varieties in the Eastern Himalayan region of NE India are cultivated in diverse eco-climatic condition in different seasons of the year. A wide range of morphological variation and grain qualities exist among the indigenous rice varieties of the region. However, preference for cultivation of high yielding agriculturally improved varieties is posing a threat to the indigenous rice gene pool of the region. Understanding the genetic diversity and population structure is important for developing conservation strategies and sustainable utilization of rice genetic resources.

In Chapter 1, genetic diversity and population structure of indigenous rice varieties were studied using SSR markers. Very high levels of genetic diversity, comparable to that of wild rice populations from other regions of the world, were detected among rice varieties traditionally cultivated in the Eastern Himalayan region of NE India. Sali ecotype showed the highest genetic diversity among ecotypes. Genetic diversity among indigenous varieties was much higher than the agronomically improved counterparts. Within variety genetic diversity among different indigenous rice varieties was also revealed in this study. This demonstrated the need for conservation of multiple individuals of the same variety to maintain the genetic variation among the traditional varieties. The study showed two major groups of rice varieties among the indigenous varieties. Though different ecotypes such as Boro, jhum and Sali were included in the present study, no detectable genetic clustering among or within these types was found.

The traditional method of rice classification into indica and japonica is largely based on morphology or cultivation type. However, such classification is often influenced by growing and local environmental conditions. In Chapter 2, I used indel markers
specifically designed from indica and japonica whole genome sequences and classified rice varieties to two groups based on allele frequency data. The study showed that different ecotypes such as Sali, Boro and jhum primarily fall into either indica or japonica subspecies. A few indigenous varieties were found intermediate between the two groups. It demonstrated that indigenous rice varieties of Eastern Himalayan region in NE India are predominately indica type. Morphology or ecotype based classification did not correspond with the indel marker based classification in this study.

In Chapter 3, I studied two genes ( $W x$ and $O s C 1$ ) that regulate two important traits in rice. It was found that nucleotide mutations at a particular gene do not exclusively contribute for the corresponding trait phenotype, suggesting that alternative genomic regions may also be involved in determining the phenotype. Statistical analysis revealed no significant selection signatures in the sequences of either gene. However, low level of selection at certain regions of each gene was evident.

This study demonstrated very high level of genetic diversity among the indigenous rice varieties of Eastern Himalayan region in NE India. Such a rich genepool could serve as a repository of unique genes that might be harnessed to maintain the future food security in light of the changing climate. Therefore, urgent need for conservation of indigenous rice varieties is warranted before they are lost forever. Further studies based on genome wide patterns of nucleotide diversity are needed to better understanding the nature of rice gene pools of NE India for future use and conservation.

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## APPENDICES

## Appendix 1: Aligned nucleotide sequence data matrix of the $\boldsymbol{W} \boldsymbol{x}$ gene


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Papue
Lahi
Joha
Local Basmati
Sorpuma
Kawanglawang
Borjahinga
Til Bora
Hati Hali
Ranjit
Kakiberoin
Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
Bashful

| 60 | 70 | 80 | 90 |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |
| CTTAGATGAACI | T-T | TG | T |  | 97] |
| CTTAGATGAAC | TT-T | TTGC | CCTA |  | [97] |
| CTTAGATGAAC | TT-T | TTG | CT |  | [97] |
| CTTAGATGAAC |  |  |  |  | [97] |
| CTTAGATGAACI | TT-T | TTGC | CCTA |  | [97] |
| CTTAGATGAAC | TT-T | TTG | CT |  | [97] |
| CTTAGATGAACI | TT-T | TTGC | CCTA |  | [97] |
| CTTAGATGAACT | TT-T | TTG | CCTA |  | [97] |
| CTTAGATGAAC | T- |  |  |  | [97] |
| CTTAGATGAAC | TT-T | TTGC | CCTA |  | ] |
| TAGATGAACI | T- | TG |  |  | [97] |
| CTTAGATGAACI | TTAT | TTGC | CCTA |  | [98] |
| GATGAA | TTA | TTG |  |  | 8] |
| CTTAGATGAACI | T-T | TG | CT |  | [97] |
| CTTAGATGAAC | TT-T | TTGC |  |  | [97] |
| CTTAGATGAAC | TT-T | TTGC | CT |  | [97] |
| CTTAGATGAAC | TT-T |  |  |  | [97] |
| CTTAGATGAAC | TT-T | TTGC | CCTA |  | [97] |
| CTTAGATGAACI | T- | TG |  |  | [97] |
| TAGATGAAC |  |  |  |  | [97] |

Moircha
Joya
Bas Beroin
Ranga Borah
Mulahail
Guaroi
Mimutim
Harinarayn
Bherapawa
O. rufipogon
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Lahi
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Local Basmati
Sorpuma
Kawanglawang
Borjahinga
Til Bora
Hati Hali
Ranjit
Kakiberoin
Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
Bashful
Moircha
Joya
Bas Beroin
Ranga Borah
Mulahail
Guaroi
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Sorpuma
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Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa

CTTAGATGAACTTATTCCTT-TTTATATTTGC-ACAGGCCTAATTT-CAA CTTAGATGAACTTATTCCTT-TTTATATTTGC-ACAGGCCTAATTT-CAA CTTAGATGAACTTATTCCTT-TTTATATTTGC-ACAGGCCTAATTT-CAA CTTAGATGAACTTATTCCTT-TTTATATTTGC-ACAGGCCTAATTT-CAA CTTAGATGAACTTATTCCTT-TTTATATTTGC-ACAGGCCTAATTT-CAA CTTAGATGAACTTATTCCTT-TTTATATTTGC-ACAGGCCTAATTT-CAA CTTAGATGAACTTATTCCTT-TTTATATTTGC-ACAGGCCTAATTT-CAA CTTAGATGAACTTATTCCTT-TTTATATTTGC-ACAGGCCTAATTT-CAA CTTAGATGAACTTATTCCTT-TTTATATTTGC-ACAGGCCTAATTT-CAA CTTAGATGAACTTATTCCTT-TTTATATTTGCTACAGGCCTAATTTGCAA
110120130140 150]

GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT [146] GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT [146] GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT [146] GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT [146] GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT [146] GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT [146] GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAATTCTCTC-TAGCTTATT GTCCAGCCCAGCTTTCTTCAGCCTGTTTGATAAGTCTCTCATAGCTTATT
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ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA
ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA
ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA
ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA
ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA
ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA
ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA
ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA
ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA ACAGCCG-TGGGAGAGGAGATATACAGCTACAAGATTACAAGTCGATGTA
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Bahadur
Pankaj
Bashful
Moircha Joya
Bas Beroin
Ranga Borah Mulahail
Guaroi
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O. rufipogon
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Local Basmati
Sorpuma
Kawanglawang
Borjahinga
Til Bora
Hati Hali
Ranjit
Kakiberoin
Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
Bashful
Moircha
Joya
Bas Beroin
Ranga Borah
Mulahail
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Balam
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| 610 | 620 | 630 | 640 | $650]$ |
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| 660 | 670 | 680 | 690 | $700]$ |
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| 710 | 720 | 730 | 740 | $750]$ |
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GCTCGCGGCGCGCCACC---AAACT-GGCAGGCACTCAGCTCGCTGCTGG [739]
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GCTCGCGGCGCGCCACC---AAACT-GGCAGGCACTCAGCTCGCTGCTGG
GCTCGCGGCGCGCCACCCCAAAACT-GGCAGCCACTCAGCTCGCTGCTGG

| 760 | 770 | 780 | 790 | $800]$ |
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| 1060 | 1070 | 1080 | 1090 | 110 |
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| $\cdot$ | $\cdot$ | $\dot{C}$ | $\dot{C}$ | .$]$ | GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC [1077] GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCA----GCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC GCCACCAGCGTGCGTGCGGTGCAATGCAACGTACGCCAAGCCGAAACGGC

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| 1110 | 1120 | 1130 | 1140 | $1150]$ |
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AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA [1127] AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA [1127] AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA [1127] AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA [1127] AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AgGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA

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AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCATCGCGCACGCACGCACACACAGGCCACAGCACACGCGAGCGA AGGCAGCACCGCGCGCGCACGCACGCAC---------------------------
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| 1160 | 1170 | 1180 | 1190 | $1200]$ |
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CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC [1177] CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC CGTACGCGAGTGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC ---ACGCGAGAGCATGCAGATGCATGCGCGGGGCTCGCGCGAGACCGGCC

| 1210 | 1220 | 1230 | 1240 | $1250]$ |
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GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC [1220] GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC------GTCGTC [1220] GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC [1220] GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC [1220] GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC [1222] GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC [1220] GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC [1223] GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC [1220] GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC [1220] GATGGG-TTCGCTTCTC-TTСTСтСTCCCGTCCCGTTGC-----GTCGTC GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC GATGGG-TTCGCTTCTC-TTCTCTCTCCCGTCCCGTTGC-----GTCGTC
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ATAGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGCTCTGAGGCACTG ATAGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGCTCTGAGGCACTG ATAGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGCTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATAGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGCTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATAGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGCTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTAGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATAGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGCTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATAGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGCTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGTTCTGAGGCACTG ATAGAC-AAAAGTCGGTTTTGCTTTTAGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTAGTTTTTT-GGTTCTGAGGCACTG ATAGAC-AAAAGTCGGTTTTGCTTTTGGTTTTTT-GGCTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTAGTTTTTT-GGTTCTGAGGCACTG ATGGAC-AAAAGTCGGTTTTGCTTTTAGTTTTTT-GGTTCTGAGGCACTG ATGGACAAAAAGTCGGTTTTGCTTTTGGTTTTTTGGGTTCCGAGGCACTG
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ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC [1318] ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC [1318] ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC [1318] ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC [1318] ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC

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ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC ACGTGCGGGCCAGCGTACGCCTGCGTGCCCCGCATGTCATCGTCGACACC
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| 1360 | 1370 | 1380 | 1390 | $1400]$ |
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GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG [1368] GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG [1368] GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG [1368] GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG [1368] GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGAGAAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGCGGGAGGGAGAGGGGGAGAGAGAG GGCCGGGGACCGGGTAAAATGTGTTGC----------GGGGGAGAGAGAG

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| 1410 | 1420 | 1430 | 1440 | $1450]$ |
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ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA [1418] ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA [1418] ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA [1418] ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA
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ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA ATCGCGCGGGCTTCACGCAACGGCGCTACAAATAGCCACCCACACCACCA
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| 1460 | 1470 | 1480 | 1490 | $1500]$ |
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CCCCCTCTCTCACCATTCCTTCAGTTCTTTGTCTATCTCAAGACACAAAT [1468] CССССТСTCTCACCATTCCTTCAGTTCTTTGTCTATCTCAAGACACAAAT [1468] СССССТСТСТСАССАТTССТTCAGTTCTTTGTCTATCTCAAGACACAAAT [1468] СССССТСТСТСАССАTTССТTCAGTTCTTTGTCTATCTCAAGACACAAAT [1468] СССССТСТСТСАССАTTССТTCAGTTCTTTGTCTATCTCAAGACACAAAT [1470] СССССТСтСтСАССАттССТТСАGTTCTTTGTСТАТСТСААGACACAAAT [1468] СССССТСТСТСАССАTTССТTCAGTTCTTTGTCTATCTCAAGACACAAAT [1471] CCCCCTCTCTCACCATTCCTTCAGTTCTTTGTCTATCTCAAGACACAAAT [1468] CCCCCTCTCTCACCATTCCTTCAGTTCTTTGTCTATCTCAAGACACAAAT [1468] СССССТСTСТСАССАTTCCTTCAGTTCTTTGTCTATCTCAAGACACAAAT [1470] СССССТСТСТСАССАТTССТTCAGTTCTTTGTCTATCTCAAGACACAAAT [1468] CCCCCTCTCTCACCATTCCTTCAGTTCTTTGTCTATCTCAAGACACAAAT [1471] СССССТСТСТСАССАТТССТTCAGTTCTTTGTCTATCTCAAGACACAAAT [1471] СССССТСТСТСАССАТТССТTCAGTTCTTTGTCTATCTCAAGACACAAAT [1470] СССССТСТСТСАССАТТССТTСАGTTCTTTGTCTATCTCAAGACACAAAT [1470] СССССТСТСТСАССАТТССТTСАGTTCTTTGTCTATCTCAAGACACAAAT [1470] СССССТСТСТСАССАТТССТTСАGTTСTTTGTCTATCTCAAGACACAAAT [1471] СССССТСТСТСАССАТТССТTСАGTTCTTTGTCTATCTCAAGACACAAAT [1470] СССССТСТСТСАССАТTССТTCAGTTCTTTGTCTATCTCAAGACACAAAT [1470] СССССТСТСТСАССАТTССТTСАGTTCTTTGTCTATCTCAAGACACAAAT [1468] СССССТСТСТСАССАTTCСTTCAGTTCTTTGTCTATCTCAAGACACAAAT СССССТСТСТСАССАТTCCTTCAGTTCTTTGTCTATCTCAAGACACAAAT СССССТСТСТСАССАТTССТTСАGTTCTTTGTCTATCTCAAGACACAAAT СССССТСтСТСАССАтTССТTСАGTTCTTTGTCTATCTCAAGACACAAAT СССССТСТСТСАССАТTССТTСАGTTCTTTGTCTATCTCAAGACACAAAT СССССТСТСТСАССАТTССТTСАGTTCTTTGTCTATCTCAAGACACAAAT СССССТСТСТСАССАТTССТTСАGTTСTTTGTСТАТСТСААGACACAAAT СССССТСТСТСАССАTTCСTTCAGTTCTTTGTCTATCTCAAGACACAAAT СССССТСTСTCACCATTCCTTCAGTTCTTTGTCTATCTCAAGACACAAAT СССССТСТСТСАССАТТССТTСАGTTCTTTGTСТАТСТСААААСАСАААТ [1397]

| 1510 | 1520 | 1530 | 1540 | $1550]$ |
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CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG [1568]
CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG
CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG СTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTGTTCTGTTGTTCATCAGGAAGAACATCTG CTTCACTTCTCTGCTTGTGTTCTTCTGTTGTTCATCAGGAAGAACATCTG
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CAAGGTATACA----TATATGTTTATAATTCTTTGT-TTCCCCTCTTATT [1613]
CAAGGTATACA----TATATGTTTATAATTCTTTGT-TTCCCCTCTTATT [1607]
CAAGGTATACA----TATATGTTTATAATTCTTTGT-TTCCCCTCTTATT [1609]
CAAGGTATACA----TATATGTTTATAATTCTTTGT-TTCCCCTCTTATT [1595]
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CAAGGTATACATGTATATATGTTTATAATTCTTTGTTTTCCCCCCTTCTT [1527]
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CAGATCGATCACATGCATCTTTCATTGCTCGTTTTTCCTTACAAATAGTC
CAGATCGATCACATGCATCTTTCATTGCTCGTTTTTCCTTACAAGTAGTC

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| 1860 | 1870 | 1880 | 1890 |
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| AGTCTAGAGAAACACACCCAGGGGTTTTCCAACTAGCTCCACA-AGATGG |  |  |  |
| AGTCTAGAGAAACACACCCAGGGGTTTCCAACTAGCTCCACA-AGATGG | $[1849]$ |  |  |
| AGTCTAGAGAAACACACCCAGGGGTTTTCCAACTAGCTCCACA-AGATGG | $[1843]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1845]$ |  |  |
| AGTCTAGAGAAACACACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1829]$ |  |  |
| AGTCTAGAGAAACACACCCAGGGGTTTTCCAACTAGCTCCACA-AGATGG | $[1843]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1838]$ |  |  |
| AGTCTAGAGAAACACACCCAGGGGTTTTCCAACTAGCTCCACA-AGATGG | $[1843]$ |  |  |
| AGTCTAGAGAAACACACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1845]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1837]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1835]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1838]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1838]$ |  |  |
| AGTCTAGAGAAACACACCCAGGGGTTTTCCAACTAGCTCCACA-AGATGG | $[1845]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1837]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1837]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1838]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1837]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1839]$ |  |  |
| AGTCTAGAGAAACACACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1827]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1837]$ |  |  |
| AGTCTAGAGAAACATACCCAGGGGTTTTCCAGCTAGCTCCACA-AGATGG | $[1837]$ |  |  |

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. $\quad . \quad$. IGGGCTAGCTGACCTAGATTTGAAGTCTCACTCCTTATAATTATTTTATA [1899] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCCTTATAATTATTTTATA [1893] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCCTTATAATTATTTTATA [1895] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1884] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCTTTCTAATTATTTGATA [1879] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCCTTATAATTATTTTATA [1893] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1887] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCCTTATAATTATTTTATA [1893] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1894] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1886] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1884] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1887] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1887] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCCTTATAATTATTTTATA [1895] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCCTTCTAATTATTTGATA [1886] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1886] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1887] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1886] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1888] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCTTTCTAATTATTTGATA [1877] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1886] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1886] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCCTTATAATTATTTTATA [1893] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1886] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCTTTCTAATTATTTGATA [1877] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1892] TGGGCTAGCTGACCTAGATTTGAAGTCTCACTCCTTATAATTATTTTATA [1895] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1893] TGGGCTAGCTGACCTAGATTT-AAGTCTCACTCTTTCTAATTATTTGATA [1892] TGGGCTAACTGACCTGGATTCGAGACCTCACTCCTTTTAATTATTTGATA [1823]

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TTAGATCATTTTCTAATATTCGTGTCTTTTTTTATTCTAGAGTCTAGATC [1949]
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Lallatoi
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| 2060 | 2070 | 2080 | 2090 | $2100]$ |
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TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2048]
TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2042] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2044] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2033] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2028] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2042] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2036] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGA-TGAAATTCACA [2041] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2043] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2035] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA [2033] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGA-TGAAATTCACA [2035] TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGA-TGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA

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TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGA-TGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGA-TGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGA-TGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGA-TGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGA-TGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGATTGAAATTCACA TCAGGAGGGTTTATTTTGGGTATAGGTCAAAGCTAAGGTTGAAATCCACA
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AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG [2098]

AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG AATAGTAAAATCAGAATCCAACCAATTTTAGTAGCCGAGTTGGTCAAAGG
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AAAATGTATATAGCTAGATTTATTGTTTTGGCAAAAAAAAATCTGAATAT [2148]
AAAATGTATATAGCTAGATTTATTGTTTTGGCAAAAAAAAATCTGAATAT [2142]
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Borua Beroin
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Balam
Borua Beroin
Lallatoi
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TTTTTTAAAAAAAAAACTTTGGTCTTATTTTTGAACGTTTTAAGTTTCA- [2466]
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TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2580]
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TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2571]
TG-TCTTTTTTTTTTCGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2566]
TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2580]
TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2574]
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TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2580]
TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2573]
TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2571]
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TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2572]
TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2572]
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TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2577]
TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2581]
TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2580]

Bherapawa
O. rufipogon
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Papue
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Borjahinga
Til Bora
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Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
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Joya
Bas Beroin Ranga Borah Mulahail

TG-TCTTTTTTTTT-CGAATTTTAAATGTAGCTTCAAATTCTAATCCCCA [2578] TGTTGTTTTTTTTTTCGAATTTTAAATGTAGCTTCAAATCCTAATCCCCA
[2516]

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| 2710 | 2720 | 2730 | 2740 | $2750]$ |
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| Mimutim | TATTTGAAAACC-AGTTCAAA | CTTTTAG |
| Harinarayn | TATTTGAAAACC-AGTTCAA | CTTTTAG |
| Bherapawa | TATTTGAAAACC-AGTTCAA | CTTTTAG |
| O. rufipogon | TATTTCAAAACC-AGTTCAA | TTTTAG |
| [ | 2760 |  |
| [ | . . |  |
| Papue | TTCAATTCAGTGCAGAGATC | [2704] |
| Lahi | TTCAATTCAGTGCAGAGATC | [2698] |
| Joha | TTCAATTCAGTGCAGAGATC | [2700] |
| Local Basmati | TTCAATTCAGTGCAGAGATC | [2690] |
| Sorpuma | TTCAATTCAGTGCAGAGATC | [2686] |
| Kawanglawang | TTCAATTCAGTGCAGAGATC | [2698] |
| Borjahinga | TTCAATTCAGTGCAGAGATC | [2693] |
| Til Bora | TTCAATTCAGTGCAGAGATC | [2698] |
| Hati Hali | TTCAATTCAGTGCAGAGATC | [2700] |
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| Kakiberoin | TTCAATTCAGTGCAGAGATC | [2690] |
| Aubalam | TTCAATTCAGTGCAGAGATC | [2691] |
| Balam | TTCAATTCAGTGCAGAGATC | [2692] |
| Borua Beroin | TTCAATTCAGTGCAGAGATC | [2700] |
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| IR8 | TTCAATTCAGTGCAGAGATC | [2691] |
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| Bahadur | TTCAATTCAGTGCAGAGATC | [2692] |
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| Moircha | TTCAATTCAGTGCAGAGATC | [2691] |
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| Bas Beroin | TTCAATTCAGTGCAGAGATC | [2699] |
| Ranga Borah | TTCAATTCAGTGCAGAGATC | [2692] |
| Mulahail | TTCAATTCAGTGCAGAGATC | [2682] |
| Guaroi | TTCAATTCAGTGCAGAGATC | [2696] |
| Mimutim | TTCAATTCAGTGCAGAGATC | [2700] |
| Harinarayn | TTCAATTCAGTGCAGAGATC | [2699] |
| Bherapawa | TTCAATTCAGTGCAGAGATC | [2697] |
| O. rufipogon | TTCAATTCAGTGCAGAGATC | [2635] |

## Appendix 2: Aligned nucleotide sequence data matrix of the $O s C 1$ gene



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Mulahail
Guaroi Mimutim Harinarayan Bherapawa
``` O. rufipogon
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Papue
Lahi
Joha
Local Basmati
Sorpuma
Kawanglawang
Borjahinga
Til Bora
Hati Hali
Ranjit
Kakiberoin
Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
Bashful
Moircha
Joya
Basberoin
Ranga_Borah
Mulahail
Guaroi
Mimutim
Harinarayan
Bherapawa
O. rufipogon
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Papue
Lahi
Joha
Local Basmati
Sorpuma
Kawanglawang
Borjahinga
Til Bora
Hati Hali
Ranjit
Kakiberoin
Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
Bashful
Moircha

GACGAGCAAGGAGGACGACGTGCTTGCCTCCTACATCAAGTCCCATGGCG GACGAGCAAGGAGGACGACGTGCTTGCCTCCTACATCAAGTCCCATGGCG GACGAGCAACGAGGACGACGTGCTTGCCTCCTACATCAAGTCCCATGGCG GACGAGCAAGGAGGACGACGTGCTTGCCTCCTACATCAAGTCCCATGGCG GACGAGCAAGGAGGACGACGTGCTTGCCTCCTACATCAAGTCCCATGGCG GACGAGCAAGGAGGACGACGTGCTTGCCTCCTACATCAAGTCCCATGGCG
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Joya
Basberoin Ranga Borah Mulahail Guaroi Mimutim Harinarayan Bherapawa O. rufipogon
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Papue
Lahi
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Lallatoi
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Bashful
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TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749]
TACTGCCGGTTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [750]
TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749]
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TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749]
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TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749]
TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749]
TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCGTTTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [750] TACTGCCGTTTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [750] TACTGCCGTTTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [750] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749] TACTGCCG-TTTTGATCGATCGTGTATATATGTTGTCAGGTGGTCTCTCA [749]


TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACT----- [794] TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG [799] TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG
\begin{tabular}{|c|c|c|}
\hline Local Basmati & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACT & [795] \\
\hline Sorpuma & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACT & [794] \\
\hline Kawanglawang & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG & [799] \\
\hline Borjahinga & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG & [799] \\
\hline Til Bora & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG & [799] \\
\hline Hati_Hali & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG & [799] \\
\hline Ranjīt & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACT & [794] \\
\hline Kakiberoin & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAAC & [794] \\
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\hline Balam & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG & [799] \\
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\hline Lallatoi & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACT & [795] \\
\hline IR8 & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACI & [795] \\
\hline Arfa & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAAC & [794] \\
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\hline Moircha & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAAC & [794] \\
\hline Joya & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAAC & [794] \\
\hline Basberoin & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG & [799] \\
\hline Ranga Borah & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACI & [794] \\
\hline Mulahail & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACT & [794] \\
\hline Guaroi & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACI & [794] \\
\hline Mimutim & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACI & [794] \\
\hline Harinarayan & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACT & [794] \\
\hline Bherapawa & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG & [799] \\
\hline O. rufipogon & TTGCAGGCAGGCTGCCGGGCCGAACAGACAATGAAATCAAGAACTACTGG & [799] \\
\hline [ & 810820830 840 80 & \\
\hline [ & .] & \\
\hline Papue & CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
\hline Lahi & AACAGCACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [849] \\
\hline Joha & AACAGCACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [849] \\
\hline Local Bas & -----CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [840] \\
\hline Sorpuma & CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
\hline Kawanglawang & AACAGCACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCTGCCGG & [849] \\
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\hline Til Bora & AACAGCACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCTGCCGG & [849] \\
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\hline Ranjit & CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
\hline Kakiberoin & -CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
\hline Aubalam & -CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
\hline Balam & AACAGCACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCTGCCGG & [849] \\
\hline Borua Beroin & AACAGCACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [850] \\
\hline Lallatoi & -CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [840] \\
\hline IR8 & -CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [840] \\
\hline Arfa & --CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
\hline Bahadur & -CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
\hline Pankaj & -----CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
\hline Bashful & AACAGCACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [849] \\
\hline Moircha & -----CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
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\hline Ranga Borah & CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
\hline Mulahail & -CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
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\hline Mimutim & -CACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [839] \\
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\hline Bherapawa & AACAGCACGCTCAGCCGCAAGATCGGCACCGCCGCCACCGCCGCCGCCGG & [849] \\
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\hline [ & 860 & 870 & 880 & 890 900 & \(900]\) \\
\hline [ & & & & & \\
\hline Papue & CAGCCGCGGTGGC & GCCGG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Lahi & CAGCCGCGGTGGC & GCCG & GCCA & CGGACGCGGCGT & [899] \\
\hline Joha & CAGCCGCGGTGGC & GCCGG & GCCAG & CGGACGCGGCGT & [899] \\
\hline Local Basmati & CAGCCGCGGTGG & GCCGG & GCCAG & CGGACGCGGCGT & [890] \\
\hline Sorpuma & CAGCCGCGGTGG & GCCGG & GCCA & CGGACGCGGCGT & [889] \\
\hline Kawanglawang & CAGCCGCGGTGGC & GCCGG & GCCAG & GGACGCGGCGT & [899] \\
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\hline Ranjit & CAGCCGCGGTGGC & GCCGG & GCCA & CGGACGCGGCGT & [889] \\
\hline Kakiberoin & CAGCCGCGGTGGC & GCCGG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Aubalam & CAGCCGCGGTGGC & GCCGG & GCCA & CGGACGCGGCGT & [889] \\
\hline Balam & CAGCCGCGGTGG & GCCGG & GCCAG & CGGACGCGGCGT & [899] \\
\hline Borua Beroin & CAGCCGCGGTGGC & & GCCAG & CGGACGCGGCGT & [900] \\
\hline Lallatoi & CAGCCGCGGTGG & GCCGG & GCCA & CGGACGCGGCGT & [890] \\
\hline IR8 & CAGCCGCGGTGGC & GCCG & GCCAG & CGGACGCGGCGT & [890] \\
\hline Arfa & CAGCCGCGGTGGC & GCCG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Bahadur & CAGCCGCGGTGGC & GCCG & GCCA & CGGACGCGGCGT & [889] \\
\hline Pankaj & CAGCCGCGGTGG & GCCGG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Bashful & CAGCCGCGGTGGC & GCCG & GCCA & CGGACGCGGCGT & [899] \\
\hline Moircha & CAGCCGCGGTGG & GCCG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Joya & CAGCCGCGGTGG & GCCGG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Basberoin & CAGCCGCGGTGG & GCCG & GCCAG & CGGACGCGGCGT & [899] \\
\hline Ranga Borah & CAGCCGCGGTGG & GCCGG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Mulahail & CAGCCGCGGTGG & GCCG & GCC & GGACGCGGCGT & [889] \\
\hline Guaroi & CAGCCGCGGTGG & GCCGG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Mimutim & CAGCCGCGGTGGC & GCCG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Harinarayan & CAGCCGCGGTGG & GCCG & GCCAG & CGGACGCGGCGT & [889] \\
\hline Bherapawa & CAGCCGCGGTGG & GCCG & GCCAG & CGGACGCGGCGT & [899] \\
\hline O. rufipogon & CAGCCGCGGTGGC & GCCG & GCCA & CGGACGCGGCGT & [899] \\
\hline [ & 910 & 920 & 930 & 940 & \\
\hline [ & & & & & \\
\hline Papue & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [939] \\
\hline Lahi & CGTCCAGCTCCG & CGCC & GCAG & CAGCCTCCCGC & [949] \\
\hline Joha & CGTCCAGCTCCG & GGCC & GCAGC & CCAGCCTCCCGC & [949] \\
\hline Local Basmati & CGTCCAGCTCCG & cGCC & GCAGC & CCAGCCTCCCGC & [940] \\
\hline Sorpuma & CGTCCAGCTCCG & cGCC & GCAGC & CAGCCTCCCGC & [939] \\
\hline Kawanglawang & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [949] \\
\hline Borjahinga & CGTCCAGCTCC & CGCC & CAG & CAGCCTCCCGC & [949] \\
\hline Til Bora & CGTCCAGCTCCG & cGCC & GCAGC & CCAGCCTCCCGC & [949] \\
\hline Hati Hali & CGTCCAGCTCCG & cGCC & GCAGC & CCAGCCTCCCGC & [949] \\
\hline Ranjit & CGTCCAGCTCCG & GGCC & GCAG & CAGCCTCCCGC & [939] \\
\hline Kakiberoin & CGTCCAGCTCCG & cGCC & GCAGC & CCAGCCTCCCGC & [939] \\
\hline Aubalam & CGTCCAGCTCCG & cGCC & GCAGC & CCAGCCTCCCGC & [939] \\
\hline Balam & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [949] \\
\hline Borua Beroin & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [950] \\
\hline Lallatoi & CGTCCAGCTCCG & GCC & CAGC & CAGCCTCCCGC & [940] \\
\hline IR8 & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [940] \\
\hline Arfa & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [939] \\
\hline Bahadur & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [939] \\
\hline Pankaj & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [939] \\
\hline Bashful & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [949] \\
\hline Moircha & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [939] \\
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\hline Basberoin & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [949] \\
\hline Ranga Borah & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [939] \\
\hline Mulahail & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [939] \\
\hline Guaroi & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [939] \\
\hline Mimutim & CGTCCAGCTCCG & CGCC & GCAGC & CCAGCCTCCCGC & [939] \\
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\end{tabular}

Harinarayan Bherapawa O. rufipogon
[
Papue
Lahi
Joha
Local Basmati
Sorpuma
Kawanglawang
Borjahinga
Til Bora
Hati Hali
Ranjit
Kakiberoin
Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
Bashful
Moircha
Joya
Basberoin
Ranga Borah
Mulahail
Guaroi
Mimutim
Harinarayan
Bherapawa
O. rufipogon
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[
Papue
Lahi
Joha
Local Basmati
Sorpuma
Kawanglawang
Borjahinga
Til Bora
Hati Hali
Ranjit
Kakiberoin
Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
Bashful
Moircha
Joya
Basberoin
Ranga Borah

CGTCCAGCTCCGTCGTGCCGCCGGGCCAGCAGCAGCAGCCAGCCTCCCGC CGTCCAGCTCCGTCGTGCCGCCGGGCCAGCAGCAGCAGCCAGCCTCCCGC CGTCCAGCTCCGTCGTGCCGCCGGGCCAGCAGCAGCAGCCAGCCTCCCGC
\begin{tabular}{lllll}
960 & 970 & 980 & 990 & \(1000]\) \\
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\end{tabular}

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\begin{tabular}{lllll}
1010 & 1020 & 1030 & 1040 & \(1050]\) \\
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\([1049]\)
\([1039]\)

Mulahail
Guaroi
Mimutim
Harinarayan
Bherapawa O. rufipogon
[
Papue
Lahi
Joha
Local Basmati
Sorpuma
Kawanglawang
Borjahinga
Til Bora
Hati Hali
Ranjit
Kakiberoin
Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
Bashful
Moircha
Joya
Basberoin
Ranga Borah
Mulahail
Guaroi
Mimutim
Harinarayan
Bherapawa
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Papue
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Local Basmati
Sorpuma
Kawanglawang
Borjahinga
Til Bora
Hati Hali
Ranjit
Kakiberoin
Aubalam
Balam
Borua Beroin
Lallatoi
IR8
Arfa
Bahadur
Pankaj
Bashful
Moircha

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\begin{tabular}{lllll}
1110 & 1120 & 1130 & 1140 & \(1150]\) \\
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[^0]:    © Baharul Choudhury, 2013

