SciMedCentral International Journal of Plant Biology & Research

Review Article

Origin, Distribution and Heading date in Cultivated Rice

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Submitted: 10 February 2014
Accepted: 25 February 2014
Published: 26 February 2014
ISSN: 2333-6668

Keywords
- Oryza sativa
- Quantitative traits locus
- Ecosystem and wild species

Abstract

Rice is one of the most important global food crops and a primary source of calories for more than half of the world's population. There are two cultivated and twenty-one wild species of genus Oryza. O. sativa, the Asian cultivated rice is grown all over the world. The African cultivated rice, O. glaberrima is grown on a small scale in West Africa. The genus Oryza probably originated about 130 million years ago in Gondwanaland and different species got distributed into different continents with the breakup of Gondwanaland. The cultivated species originated from a common ancestor with AA genome. Perennial and annual ancestors of O. sativa are O. rufipogon and O. nivara and those of O. glaberrima are O. longistaminata, O. breviligulata and O. glaberrima probably domesticated in Niger River delta. Varieties of O. sativa are classified into six groups on the basis of genetic affinity. Rice production increased steadily during the green revolution era primarily as a result of introducing high-yielding rice varieties. World rice production increased at a rate of 2.3–2.5% per year during 1970s and 1980s, but this rate of growth was only 1.5% per year during the 1990s. The yield growth rate for rice has further declined during the first decade of this century. However, the populations in the major rice-consuming countries continue to grow at a rate of more than 1.5% per year. According to various estimates, world rice production must increase at the rate of 2 million tons per year. To meet this challenge, rice varieties with higher yield potential and greater yield stability are needed. Various strategies for increasing the yield potential of rice include; conventional hybridization and selection, F1 hybrid breeding, modification of plant architecture, and enhancement of photosynthesis. Many genes and QTLs have recently been identified which will assist with rice breeding objectives.

INTRODUCTION

Rice is the world's most important food cereal crop and a main food source for more than a third of the world's population [1]. More than 90% of the world's rice is cultivated and consumed in Asia where 60% of the world's people live [1]. Rice provide about 35 to 60% of the calories consumed by 3 billion Asians [1]. Rice is grown on about 148 million hectares annually, or on 11% of the world's cultivated land [1]. Rice is the only major cereal crop that is consumed almost exclusively by humans [1]. Earth's rice production was 553 million tons in 1996 [1]. China, the largest producer, produced 187 million tons followed by India (122 million tons), Indonesia (50million tons), Bangladesh (27 million tons), Vietnam (24million tons), Thailand (21million tons) and Myanmar (20 million tons) [1]. But only about 4% of the world's rice production is traded internationally [1]. Thailand is world's leading rice exporter, selling about 4–6 million tons yearly [1]. The United States is the second largest exporter, even though it ranks 11th in production [1]. It produces 6 million tons yearly and market about 40% of it. Vietnam, Pakistan and Myanmar each market about a million tons yearly. India market about 4 million tons in 1995 while decline in 1996 but market only about 2 million tons. Iran, Iraq and Saudi Arabia are the main foreign buyers, taking about 0.9, 0.7, and 0.5 million tons annually [1]. African countries, where demand for rice is increasing at a rate of about2%yearly, buy around 3million tons or about 25% of the total world imports each year. The importance of rice in the diet varies among countries [2]. It provide over 70% of the daily calorie intake in countries such as Bangladesh, Cambodia, Laos, and Myanmar but drops to about 40% in countries such as China and India whose northern areas consume more wheat [1]. Rice is also an important staple in Latin America, Africa and Middle East [3].The number of rice consumption is increasing at the rate of 1.5% annually where as it production at present increase only at the rate of 1.0% annually [4]. According to the United Nation (UN) estimation, the world population will increased from 6.7 billion at present to about 8 billion by 2025, therefore its production must increased from 440 million tons at present to 475 million tons by 2020 [4]. Food Agricultural Organization(FAO) estimates that by 2050 the world rice requirement will be 524 million tones which required annual increased of 2 million tons from the present level of production [4]. To meet with challenge of producing more rice from the existing land resources, therefore upland rice varieties with a highly yield potential are required, to achieve this there is need to know how photoperiod regulate flowering in rice which is the key success to a high potential yields. [4]

TAXONOMY AND ORIGIN OF CULTIVATED RICE

Of the two breed species, Asian cultivated rice, Oryza sativa, is cultivated worldwide. Oryza glaberrima, the African grown rice, is planted on a limited scale in West Africa [5]. Rice belongs to the grass family Gramineae [6]. The genus Oryza, to which grown rice belongs, may be originated at least 130 million years ago and dispersed as a wild grass in Gondwanaland, the super continent that eventually broke up and drifted apart to become Asia, Africa, Australia, and Antarctica [5]. This shows the distribution of Oryza species all over the world except Antarctica [5]. There are 22 wild species of genus Oryza, Nine of the wild species are tetraploid and the remaining wild species and the two cultivated species are diploid [5]. The universal rice, Oryza sativa, and the African rice, Oryza glaberrima, are thought to be examples of directional evolution in crop plants [5]. The wild progenitor of O. sativa is the Asian universal wild rice, O. rufipogon, which shows a range of difference from perennial to yearly types, yearly types, also given the specific name of O.nivara were tamed to become O. sativa [1]. In a parallel origin path, O. glaberrima was tamed from annual O. breviligulata, which in turn arise from perennial O. longistaminata [5]. Domestication of wild rice's probably started about 9,000 years ago [2]. Development of annuals at different elevations in East India, northern Southeast Asia, and western China was enhanced by alternating periods of drought and variations in temperature during the Neothermal Age about 10,000 to 15,000 years ago [5]. Domestication in Asia could have occurred independently and concurrently at several sites within or bordering a broad belt that extends from the plains below the eastern foothills of the Himalayas in India through upper Myanmar, northern Thailand, Laos, and Vietnam to south western or southern China [5]. The earliest and most convincing archeological evidence for domestication of rice in Southeast Asia was discovered by [5]. The African cultivar O. glaberrima originated in the Niger River delta [5]. The primary point of diversity for O. glaberrima is the swampy basin of the upper Niger River and two secondary points to the south west near the Guinean coast [5]. The primary point was probably established around 1500BC while the secondary points were formed 500 years later [5].

RICE HABITATS AND THEIR HYDROLOGICAL CONDITIONS

Rice ecosystems are usually classified into four types: irrigated, rainfed lowland, deep water and rainfed upland. Irrigated rice is the most widespread ecosystem, comprising 55% of the overall production area [3]. It is also the most productive system and is accountable for 75% of global production [3]. This can partly be explained by the reality that irrigated rice production generally takes place on well drained, fertile soils that are not subject to drought or flooding [5]. More inputs such as fertilizers are used in irrigated rice than in other ecosystems. This system has been the main focus of the Green Revolution. High levels of investment in fertilizers by farmers in irrigated systems are profitable, because the risk of crop loss due to drought or water submergence is low [5]. Deep-water rice is planted in areas that are naturally flooded to depths greater than 50cm for extended periods during the rainy season [7]. In most deep water fields, seeds are broadcast a few weeks before the beginning of the rainy season [7]. The plants can suffer from drought in the early stages of growth, but once the monsoon starts water levels rise and remain high until the end of the growing season [8]. Stems elongate following the rise in water depth, sometimes up to 3m [8]. This rice ecosystem represents about 8%of the total rice cultivation area. The main production areas are the deltas of the Ganges Brahmaputra River of India and Bangladesh, the Mekong River of Vietnam and Cambodia, the Irrawaddy River in Myanmar and the Chao Phraya River of Thailand [3]. Rainfed lowland rice is the second most important rice ecosystem, representing about 25% of total rice production area. Fields do not receive irrigation, relying entirely on rainfall or drainage from higher lands in a watershed. The defining feature of a lowland field is the bund that surrounds it, permitting water from rainfall or drainage from higher fields to be impounded [3]. Hydrological conditions in different rainfed lowland fields vary substantially depending on the position of the field in the succession of fields that drain into each other from the top to the bottom of a rice-producing watershed. In addition to the use of bunds to impound water, water is retained in many rainfed lowland fields through tillage practices designed to reduce water losses via seepage and percolation [3]. Fields are often tilled when wet (puddling), leading to the formation of a hard-pan below the soil surface [9]. This is desirable as it limits water seepage, thereby facilitating ponding of water in the field, but can also limit root growth and access to water stored in the lower regions of the soil profile [10]. Finally, rainfed upland rice is grown in unbunded fields where good soil drainage and/or uneven land surface renders the accumulation of water impossible [10]. Upland rice is usually grown in systems where little or no fertilizer is applied, and is direct seeded into unpuddled, unsaturated soil. Most traditional upland rice varieties are low-yielding and prone to lodging, but are adapted to non-flooded soils. Upland rice encompasses 12% of global rice production area and is generally the lowest-yielding ecosystem [10]. Upland rice has a proportionately greater importance in Africa and Latin America, where it accounts for around 40%22 and 45% of the rice growing areas, respectively. In Asia and Africa, upland rice farmers are among the poorest in the world and their holdings are often less than 0.5 ha in size [6]. The situation is different in Latin America since much of the upland rice production there is mechanized and farms are larger [11]. Improved upland rice varieties with higher harvest index, improved input responsiveness and higher yield potential have been developed at IRRI, in Brazil and in several Asian countries. Such 'aerobic rice' varieties combine the aerobic adaptations of traditional upland varieties with the input responsiveness, lodging tolerance and yield potential of irrigated varieties. Aerobic rice may replace irrigated rice and rainfed lowland rice in some parts of the world facing decreasing water supplies for agriculture, as is already occurring in northeast China [1]. In the irrigated and deep-water rice ecosystems, water shortage does not normally occur, but in both the rainfed upland and lowland cultivation systems drought stress are often the most important abiotic stress factor limiting yields [12]. Rainfed rice fields (both upland and lowland) within a given watershed usually drain into one another from the highest to lowest elevation [13]. The upper fields are the most droughts prone as they do not receive extra water from runoff or seepage from nearby fields. Upland rice is generally more prone to drought than lowland rice because water does not accumulate in the field, due to the lack of a bund or hard-pan layer and, often, due to irregular, sloping topography [14].

RICE CULTIVATION

Rice is grown under various growing environment. Four major environments are generally recognized as follows: Irrigated, Rainfed lowland, Upland, and lastly Flood prone.

Irrigated rice

Approximately, 55% of the world rice area planted to rice, is irrigated and is the most productive rice growing system [14]. Perhaps 75% of the world rice production comes from irrigated areas and Asian mega cities are fed from irrigated rice [14]. Irrigation water is provided by human intervention through a variety of works including river diversions, reservoirs and wells. The area of irrigated rice has expanded markedly in the last 3 decades [14]. Modern rice varieties and improved cultivation techniques have had their greatest impact on increasing the productivity of irrigated lands [15]. Most of the irrigated areas are planted to improved varieties and more fertilizer and other inputs are used than in other ecologies [15]. Rice yields in irrigated areas have more than doubled to five tons per ha in the past 30myears and there is considerable scope for further yield improvement. Irrigated areas are further divided into irrigated wet season when rainfall is supplemental with irrigation water and irrigated dry season when rainfall is very low and irrigation is the primary source of water supply [2]. Yields during the dry season are higher than during the wet season due to higher incoming solar radiation [2].

Rainfed lowland rice

About one fourth of the world rice area is rainfed lowland. Yields average about two tons per hectare [13]. Rainfed lowlands have a great diversity of growing conditions that vary by amount of rainfall and duration of rainfall, depth of standing water, duration of standing water, flooding frequency, and time of flooding, soil type and topography. Rainfed lowland fields are bunded and water is impounded, when available, just like irrigated fields. Rainfed lowlands are further subdivided into five categories [13]. Rainfed shallow favorable, where rain falls is adequate. Short periods of moisture stress may occur. Improved varieties developed for irrigated conditions are grown in such area and yields average around three tons. Rainfed shallow drought prone, where rainy period is short and periods of mild to severe drought stress occur during the growing season. Photoperiod insensitive varieties with short duration and degree of drought tolerance are most suitable [13]. Rainfed shallow submergence prone, where rice crop is submerged during periods of heavy rain falls for up to 10 days. Rainy period is generally long and crop is harvested after the rainy season is over. Photoperiod sensitive varieties are generally grown. Rainfed medium deep, where water accumulates in the fields in low lying areas and stagnates for 2 to 5 months because of impeded drainage. Photoperiod sensitive varieties with tolerance to stagnant water are grown [13].

Upland rice

Upland or dryland rice is grown under rainfed, naturally well drained soils in bunded or unbunded fields without surface water accumulation [11]. Some of the upland rice areas are on sloping mountain sides [11]. Rice is planted under dry conditions just as wheat or maize. Rice varieties are photoperiod insensitive, have deep roots and some level of drought tolerance. Many of the upland soils have low pH and are deficient in nutrients [11]. Yields average about 1.2 tons per hectare. About 16 million hectares of world rice land is classified as upland [11].

Floodprone rice

Floodprone rice is grown in low lying lands in river deltas of South and Southeast Asia. Standing water depth may vary from50 cm to more than 3m.However, flooding occurs only during part of the growing season [1]. Fields are unbunded. Rice is broadcast sown. Tall varieties with photoperiod sensitivity are grown. Varieties grown in deeper areas (100 cm) have elongation ability. About 9 million hectares are planted to floodprone rice of which 3 million falls in the category of deepwater rice [1]. Average yields are around 1.6 tons per hectare [1].

DISTRIBUTION OF CULTIVATED RICE

From the Himalayan foot hills rice spread to Western and Northern India, to Afghanistan and Iran and South to Sri Lanka [1]. The data of 2500 BC has already been mentioned for Mohenjodarao, while in Sri Lanka rice was a major crop as early as 1000 BC. The rice crop may well have been introduced to Greece and neighboring countries of Mediterranean by returning members of Alexander the Great's expedition to India in 324BC [1]. However, in all probability rice did not become an established crop in Europe much later perhaps in 15th or 16th century. Rice grown in the Mediterranean region is japonicas while the rice grown in the Indian subcontinent is indicas. Rice also travelled from India to Madagascar and East Africa and then to countries of West Africa [6]. Indica rice also spread eastward to Southeast Asia and north to China [12]. The japonica rice was most likely domesticated somewhere in northern parts of South East Asia or South China [11]. It moved north to become a temperate japonica. From China, temperate japonicas were introduced in Korea and from Korea to Japan around the beginning of 1st century. In the hilly areas of Southeast Asia japonica rice were grown under upland culture as a component of shifting cultivation before the upland tribes moved into the lowlands and introduced the japonicas into lowland culture. From mainland Southeast Asia, both indica and japonica rice were introduced into Malaysia, Philippines, and Indonesia and from Philippines to Taiwan [12]. Migrating Malays from Indonesia introduced tropical japonicas into Madagascar in 5th or 6th century. Portuguese priests introduced the tropical japonicas from Indonesia into Guinea Bissau from where they spread to other West African countries. Thus, most of upland rice varieties grown in West Africa are tropical japonicas [11]. The Portuguese also introduced tropical japonicas and lowland indicas to Brazil and Spanish people brought them to other Latin American countries. Thus, in Brazil today, most of the upland varieties are tropical japonicas and lowland varieties that belong to indica group. The first record of rice for U.S.A. dates from 1685, and it was probably introduced from Madagascar with slave trade [11].

HEADING DATE AND PHOTOPERIOD MECHANISMS

Manipulation of the heading date in rice is an important objective in all rice-breeding programs [16]. The vegetative growth duration and photoperiod sensitivity both determine the time of flowering [17]. Although a number of major genes controlling photoperiod sensitivity have been known, few of these genes have been assigned to rice chromosomes: Se-1, Se3, Se-5 on chromosome 6, E1 on chromosome 7, and E-3 on chromosome 3 [18]. Since the tagging of the first major photosensitive gene Se-1 with a molecular marker, a large number of Quantitative traits locus (QTLs) with both major and minor effects have been mapped onto rice chromosomes [19]. QTL mapping further confirmed that Se-1 locus was thesameasHd1, which explained 67% of the phenotypic variation [20]. Of four additional QT loci, Hd-2 and Hd-4 were mapped on chromosome 7 and Hd-3 and Hd-5 on chromosomes 6 and 8, respectively [20]. Three additional QTLs were identified using a BIL population of the same cross Nipponbare x Kasalath [21]. A fine mapping study using an advanced backcross progeny revealed Hd1, Hd2, and Hd3 loci as Mendelian factors [21]. Further characterization of these QTLs and their interaction were done by developing the QTL-NILs through MAS [22]. Ultimately leading to cloning and isolation of some of these QTLs [23].

ROLE OF LIGHT IN THE PHOTOPERIOD

Light performs a dual function to produce a flowering response: (1) it is necessary to entrain an endogenous oscillator called circadian clock, which in turn generates rhythms in gene expression; and (2) the presence or absence of light during particular phases of the circadian rhythm is necessary to promote or inhibit flowering, depending on the species. In rice, coincidence between darkness and an inducible phase of the circadian cycle can start the flowering process, and this mechanism is known as external coincidence. Many of the genes discussed in previous sections show rhythms of mRNA Light performs a dual function to produce a flowering response: it is necessary to entrain an endogenous oscillator called circadian clock, which in turn generates rhythms in gene expression; and the presence or absence of light during particular phases of the circadian rhythm is necessary to promote or inhibit flowering, depending on the species [24]. In rice, coincidence between darkness and an inducible phase of the circadian cycle can start the flowering process, and this mechanism is known as external coincidence [25]. Many of the genes discussed in previous sections show rhythms of mRNA expression, which are dependent on the circadian clock. Hd1 shows diurnal rhythms in mRNA accumulation both under SDs and LDs [26]. Expression always reaches a peak during the night, but under LDs the mRNA is also produced during the light phase for several hours. Induction of Hd3a expression is most effective under SDs, when transcription of Hd1 does not take place during day time. An artificial increase of Hd1 expression during the light phase by means of the 35S promoter or by Overexpression of OsGI delays flowering under short day (SD), and reduces Hd3a expression [27]. Similarly, exposure of wild-type plants to 10 min of light in the middle of a long night also results in delayed flowering and failure to induce Hd3a expression [28]. Taken together, these data suggest that coincidence of heading date 1 (Hd1) mRNA expression and light represses flowering, whereas when Hd1 is expressed during the night it promotes flowering[28]. The pattern of accumulation of Hd1 protein might explain these physiological effects, if more Hd1 protein were accumulated during the night. However, in plants overexpressing amyc-tagged Hd1 protein, accumulation of Hd1 reaches similar levels both at the end of the light phase of a short day (SD) and in the middle of the night, indicating that differential accumulation of Hd1 protein during the diurnal cycle is not the cause of delayed flowering, and that a post-translational mechanism is probably converting Hd1 into a repressor [28]. Hd1 requires PHYTOCHROME B (PhyB) to repress flowering, because phyB mutants flower early, even in plants in which Hd1 is Overexpressed by the 35S promoter [28]. Since phyB mutants, or mutants impaired in phytochrome chromophore biosynthesis such as PHOTOPERIOD SENSITIVITY 5 (SE5), do not alter rhythmic oscillation of Hd1 mRNA, it was postulated that light signals mediated by phytochromes do not affect circadian expression of Hd1, but rather modify the Hd1 protein, or a component of a transcriptional complex containing Hd1, to convert it into a repressor of flowering [29]. Consistent with this hypothesis, night breaks cannot suppress Hd3a up regulation in phyB mutants grown under SD conditions [30]. Defining the biochemical function of Hd1 protein and the molecular nature of its dual activity will provide exciting insight into the control of photoperiodic flowering. Light signals can also interfere with the molecular regulatory network through Ehd1 and Ghd7, and impose the critical day length for Hd3a expression. Physiological studies have suggested that Ehd1 induction is mediated by OsGI and blue light at dawn [31]. Pulses of blue light increase Ehd1mRNAexpression, and the effect is maximal when pulses are given in the morning and is independent of day length [31]. If OsGI mutants are exposed to blue light pulses, no induction of Ehd1 can be observed. Conversely, if plants grown under SD conditions are exposed to pulses of red light in the middle of the night, Ehd1 expression is strongly suppressed because Ghd7 is quickly up regulated [32]. Ghd7 inducibility by red light is gated around midnight under SD conditions, and at that time of the diurnal cycle is normally low [33]. Consequently, Ehd1 expression can take place in the morning. However, maximum sensitivity of Ghd7 to red light shifts to dawn under long day (LD) conditions, and this causes repression of Ehd1 [34]. In agreement with these data, se5 mutants, which are unable to produce functional phytochromes, show strongly increased expression of Ehd1 under any day length because of failure to induce Ghd7 [35]. These data indicate the existence of two inter-locked coincidence mechanisms. Ghd7 expression at dawn prevents Ehd1 expression, but as day length decreases, inducibility of Ghd7 shifts to the dark phase and de-represses Ehd1, which in turn is induced by blue light through OsGI[3]. It remains to be established which molecular components directly transmit light-quality information to the regulatory network. Light inputs to the circadian clock system can be partly mediated by OsELF3, a putative ortholog of Arabidopsis ELF3. OsELF3 was recently cloned by three groups independently, and was shown to be allelic to Ef7 and Hd17 [15]. Mutations in OsELF3 delay flowering under both SD and

LD conditions, but the strength of the phenotype depends on the mutant alleles examined and the growing conditions. The mutants show altered circadian expression of clock components including OsLHY (LATE ELONGATED HYPOCOTYL), OsPRR1 (PSEUDO RESPONSE REGULATOR 1), OsPRR37, OsPRR73, OsPRR95 and OsGI, indicating ELF3 is required to sustain their robust oscillation [36]. Diurnal patterns of gene expression are also affected under both LD and SD conditions [37]. All PRRs showed enhanced amplitude of mRNA expression in oself3 mutants, whereas OsLHY rhythmic expression is reduced[38]. OsELF3 influences photoperiodic flowering because it affects expression of regulators of Hd3a and RFT1, both in the Hd1 and Ehd1 pathways [38]. Under LD conditions, oself3 mutants increase OsGI expression, thus causing increased Hd1 expression and delayed flowering. In addition, Ghd7 expression is increased in oself3, repressing the expression of Ehd1, and ultimately, Hd3a and RFT1 [19]. Genetic data support a model by which OsELF3 promotes flowering mainly by repressing Ghd7 under SD conditions, because late flowering of oself3 mutants is corrected if Ghd7 is also mutated but not if Hd1 is mutated [20]. Conversely, under LD conditions, late flowering of oself3 can be accelerated if Ghd7 or Hd1 are mutated, suggesting that under long day lengths OsELF3 is necessary to promote flowering by maintaining low levels of these floral repressors [16].

PRODUCTION AND NUTRITIONAL CONTENTS OF RICE

Rice is the most useful cereal crop directly consumed by people. With around 600 Mt produced yearly on 149 Mha in 2003, rice provide for 23% of the world's caloric intake [3]. In the same year, wheat was cultivated on a larger area, 207 Mha, but total cultivation was slightly lower, most rice (90%) is produced in Asia, where it is estimated to supply 35–60% of the total caloric intake [3]. Rice is especially useful in the poorest Asian countries, such as Myanmar and Bangladesh, with annual per capita consumption in 2003 of 197 and 160kg, accordingly [5]. In the same year, the annual per capita consumption in the United Kingdom was 5 kg, with a world average of 54kg and an Asian average of 79kg.13 Rice-based diets generally provide low iron, zinc and vitamin A intake; these nutrient deficiencies are therefore common in regions relying on rice for most of their caloric intake [3]. Africa has roughly 3% of global rice cultivated areas and produces a relatively small amount of rice [3]. However, rice is gaining relevance on the continent, with an increase in utilization of about 6%annually [5]. Rice production areas are consequently expanding quickly to try to match the demand, but still more than 40% of the rice used in Africa is imported. Global rice cultivation increased by 130% between 1966 and 2000, while the population of low-income countries increased by an average of 90% over the same period. The world population is predicted to reach approximately 8 billion by 2030 and there is therefore a need to further increase rice yield production by 40% in the next 25years [3].

CONCLUSION

World rice production increased at a rate of 2.3–2.5% per year during 1970s and 1980s, but this rate of growth was only 1.5% per year during the 1990s. The yield growth rate for rice has further declined during the first decade of this century. However, the populations in the major rice-consuming countries continue to grow at a rate of more than 1.5% per year. According to various estimates, world rice production must increase at the rate of 2 million tons per year. To meet this challenge, rice varieties with higher yield potential and greater yield stability are needed. Various strategies for increasing the yield potential of rice include; conventional hybridization and selection, F1 hybrid breeding, modification of plant architecture, and enhancement of photosynthesis. Many genes and QTLs have recently been identified which will assist with rice breeding objectives.

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Cite this article

Dogara AM, Jumare AI (2014) Origin, Distribution and Heading date in Cultivated Rice. Int J Plant Biol Res 2(1): 1008.