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Chapter

Characterization of Wild Rice - *Oryza* Species Complexes in Sri Lanka

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Abstract

Rice is the staple food crop in Sri Lanka, which occupies 34% (0.77/million ha) of the total cultivated area. Sri Lanka currently produces 2.7 million tonnes of rough rice annually and satisfies around 95% of the domestic requirement. In Sri Lanka, genus *Oryza* consists of two species complexes, *O. sativa* (AA) and *O. officinalis* (CC). These two complexes are both pan tropical and have very similar overall distribution. Five wild rice species are reported in Sri Lanka, (*O. nivara* [AA], *O. rufipogon* (AA) *O. eichingeri* [CC], *O. rhizomatis* (CC) and *O. granulata* (GG)). *O. rhizomatis* has been reported only in Sri Lanka and considered endemic to Sri Lanka. Recent studies demonstrated, the reliance on single source of information could mislead results in the phylogenetic inferences due to analytical inconsistency and biological processes. Therefore, exact number of wild rice species in Sri Lanka becomes uncertain and the necessity arises to assess *Oryza* species complexes in Sri Lanka using morphological, anatomical, and molecular information to enumerate number of species within each *Oryza* complex and characterization of species and species complexes. The study revealed, characterization of wild rice species, to a certain extent, can be made through morphological and anatomical characters, specially lamina anatomical characters. Molecular information is more reliable in delimitation of wild rice species complexes in Sri Lanka. *O. rhizomatis* and *O. eichingeri* (CC) are well separated from the rest of wild rice species (AA). Molecular data revealed, *O. nivara* and *O. rufipogon* have undergone independent evolution within Sri Lanka. Well separated five wild rice species are existing in Sri Lanka. Studies on ecological resilience of morphological, anatomical, and molecular studies are very useful for species enumeration of wild rice complexes in Sri Lanka. The findings led to conclude that wild rice species in Sri Lanka are “ecological swarms” and represents allopatric or sympatric populations. A comprehensive knowledge on genetic diversity and population structure of wild rice germplasm in Sri Lanka provides useful information to include these locally adapted and evolved wild rice species in rice crop improvement/breeding.

**Keywords:** Wild rice, *Oryza* species complexes, Sri Lanka

1. Introduction

Rice serves as the main staple food crop of nearly half of the world’s population and it is obvious that genetic improvement of rice cultivars play an important role in the rice production for fulfilling ever increasing food demand. Rice is the staple...
food which occupies 34% (0.77/million ha) of the total cultivated area in Sri Lanka and currently produces 2.7 million tonnes of rough rice annually and satisfies around 95% of the domestic requirement [1].

The rice genus *Oryza* L. consists of ca. 21 wild and two cultivated species distributed in Asia, Africa, Australia, and the America [2, 3] and these species have been categorized into ten different genome types, such as six diploids (AA, BB, CC, EE, FF, and GG) and four allotetraploid species (BBCC, CCDD, HHJJ, and HHKK) [4, 5]. Wild rice species are important in rice breeding programs because, these species comprise traits of agronomic interest, for example, the resistance and tolerance to biotic and abiotic stresses [2, 6–8]. However, due to the sterility barriers, most of the *Oryza* germplasm is of limited use in rice breeding programs [8, 9]. Genetic resources of the AA-genome group also referred to as the *Oryza* complex, have long been a focal point of the rice breeders.

The *Oryza sativa* complex includes eight diploid species [2] and the Asian cultivated rice consists of main subspecies, *O. sativa* ssp. *Indica* and *O. sativa* ssp. *Japonica* [10–12] are of Asian origin and globally cultivated today. The two presumed wild progenitors; the perennial *O. rufipogon* (Figure 1) is distributed throughout tropical Asia and Oceania, whereas the annual *O. nivara* is distributed in tropical continental Asia (Figure 2). Another cultivated species in the genus, *O. glaberrima*, was parallelly domesticated in West Africa where it is endemic [2]. There are two additional wild species also endemic to Africa, *O. barthii* and *O. longistaminata*. The former is the annual wild progenitor of *O. glaberrima*, while the latter is a perennial, rhizomatous and partially self-incompatible grass species [13].

In Sri Lanka, the genus *Oryza* consists of two species complexes, the *O. sativa* complex that includes the AA genome species, the *O. officinalis* complex which includes the CC genome species [3, 14] and a single species *O. granulate* (GG) [15, 16]. The two complexes, *O. sativa* complex and *O. officinalis* complex are both pan tropical and have very similar overall distribution. However, only AA genome species have been cultivated and domesticated. It appears that *O. officinalis* complex species do not have the attributes that make them attractive or likely to cultivate. Of the five wild rice species reported in Sri Lanka, (*O. nivara*, *O. rufipogon* (AA); *O. eichengeri*, *O. rhizomatis* (CC); and *O. granulate* (GG)), *O. rhizomatis* grows in partially shaded areas/grass lands and has been reported only in Sri Lanka and hence considered endemic to Sri Lanka [17, 18].

![Figure 1.](image)

**Figure 1.** *O. rufipogon* (a) panicle (b) growing in a periodically drying temporary ponds.
O. rhizomatis is one of the species of the O. officinalis complex (Figure 3). The taxonomy of O. officinalis complex in Sri Lankan has been puzzling due to insufficiency of satisfactory herbarium specimens and the living plant materials. As an attempt of resolving the problem of the morphological variation in the complex, Biswal and Sharma [19] retracted the name O. collina and considered this taxon to be synonymous with O. eichingeri. Thus, Biswal and Sharma [19] agreed with both Bor [20] and Tateoka [14] that O. eichingeri is the sole representative of O. officinalis complex in Sri Lanka (Figure 4). O. officinalis in Sri Lanka grows in both shaded and open habitats, whereas O. eichingeri grows in the shade of forests in Uganda [21]. However, taxonomists were not able to give much weight to the habitat of this taxon since field notes are generally infrequent.

The new collections make known clear morphological and habitat differences in O. eichingeri and it is a larger taxon which occurs in the drier habitats in Sri Lanka [2]. This larger rhizomatous taxon has previously been called O. latifolia and O. officinalis. O. latifolia is a large non-rhizomatous tetraploid from South and Central America with broader leaves and whorled panicle branches. O. officinalis which usually has rhizomes, has smaller spikelets, shorter palea tip, more branches of approximately equal length from the lowest panicle node, and spikelets inserted away from the base of primary branches. O. officinalis is also genetically different from this Sri Lankan taxon with which it can form sterile hybrids. However, Sri Lankan taxon belongs to the same genome group as both O. officinalis and O. eichingeri, which is CC [22].

There are two diploid CC genome species in Sri Lanka, O. eichingeri and O. rhizomatis [17, 19]. Previously O. collina was the name used for Sri Lankan germplasm of the O. officinalis complex [23]. O. collina has been used for both O. eichingeri and O. rhizomatis. However, O. rhizomatis is readily distinguished from O. eichingeri by its larger plant stature and rhizome formation. O. rhizomatis appears to be intermediate between O. officinalis and O. eichingeri. Analysis of the nuclear and chloroplast genome of O. rhizomatis by RFLP and SSR reveals that O. rhizomatis differed from O. eichingeri and officinalis [24–26].

The nomenclature and the taxonomy of the elements of these complexes have been studied and nomenclatural changes have been suggested and certain de novo species was described to disentangle the problem within the complexes. Due to this reason, the exact number of wild rice species in Sri Lanka becomes uncertain and
detailed studies specially, on morphological, anatomical, and molecular aspect of the Sri Lankan wild rice are needed for the delimitation of *Oryza* complexes in Sri Lanka.

Several recent studies demonstrated that the reliance on single source of information possibly misleading the results in the phylogenetic inferences due to analytical inconsistency and biological processes [27, 28]. The inconsistencies among the

Figure 3.
(a) Panicles (b) Rhizomes (c) well-spread rhizome submerged in water of *O. rhizomatis*. (d) *O. rhizomatis* in open spaces in the dry zone (Anuradhapura District), Sri Lanka.
phylogenies have become one of the most common problems during the reconstructing molecular phylogenetics using different datasets, such as individual genes. Studies carried on the genome-wide markers have witnessed new phylogenetic reconstructions that use large quantities of genome-wide markers to illustrate former controversies on evolutionary relationships at all taxonomic levels [27–31].

In general, a gene tree does not necessarily reflect a species tree, even if the orthology of marker genes are clearly identified and employed. Therefore, many genetic markers, including unlinked loci with extensive functional representation as well as intergenic genomic regions, are needed to comprehensively track organismal history. Such a robust phylogeny will build a foundation for future insights into rice genome evolution.

Therefore, there is a need to delimit the *Oryza* species complexes in Sri Lanka using morphological, anatomical, and molecular information. The objectives of the present study are to enumerate the number of species within each *Oryza* complex (*O. sativa* complex and the *O. officinalis* complex) in Sri Lanka and characterization of species and species complexes with evidence generated from morphological, anatomical, and molecular studies.

2. Materials and methods

2.1 Seed material

A total of four wild rice species; *O. rufipogon*, *O. nivara*, *O. eichingeri* and *O. rhizomatis* were collected from different localities of the Districts, Puttalam, Anuradhapura, Vavuniya, Trincomalee, Hambantota, Matara and Ampara of Sri Lanka. The botanical names and the acronyms used were given in Table 1. The collected samples were used for morphological, anatomical and molecular studies.
2.2 Morphological studies

The morphological characterization of each species collected was based on the Plant Genetics Resource Centre (PGRC), Sri Lanka Characterization Catalogue of Rice [32] (Table 2). The leaf, culm, and rhizomes if available were collected and

| Wild Rice species | Acronym |
|-------------------|---------|
| Oryza eichingeri   | Eich    |
| O. nivara         | Niva    |
| O. rhizomatis     | Rhi     |
| O. rufipogon      | Rufi    |

Table 1.
Botanical names of the wild rice species and acronyms used in the study.

| Character Abbreviations | Character |
|------------------------|-----------|
| PLH                    | Plant Height (cm) |
| LBL                    | Leaf blade length (cm) |
| LBW                    | Leaf blade width (cm) |
| LBP                    | Leaf blade pubescence at late vegetative stage |
| LBC                    | Leaf blade color at late vegetative stage |
| BLSC                   | Basal leaf sheath color at late vegetative stage |
| LiguleL                | Ligule length at late vegetative stage (cm) |
| LiguleC                | Ligule color at late vegetative stage |
| LiguleS                | Ligule shape at late vegetative stage |
| CollorC                | collar color at late vegetative stage |
| AuricleC               | Auricle color at late vegetative stage |
| CulmL                  | Culm length (cm) |
| CulmA                  | Culm angle after flowering |
| IINCAF                 | Internode color after flowering |
| CulmS                  | Culm strength |
| PanicleL               | Panicle length |
| PanicleT               | Panicle type |
| Panicleex              | Panicle excretion |
| AWNAFH                 | Awning after full heading |
| AAWNC                  | Awn color at maturity |
| ApiculeC               | Apiculuscolor |
| SeedCC                 | Seed coat (bran) color at maturity |
| LeafS                  | Leaf senescence |
| VD                     | Vein diameter (μm) |
| IVD                    | Inter Venial distance (μm) |
processed for micro sectioning. Temporary and permanent slides were prepared for cross sections of leaves, culm and rhizomes.

2.3 Anatomical studies

The free hand sections of the collected specimens were taken and observed under the light microscope. Measurements of anatomical characteristic features were made using standard methods.

2.4 Molecular studies

Total genomic DNA was extracted from 7-day old seedlings of wild rice species; *O. rufipogon*, *O. nivara*, *O. eichingeri* and *O. rhizomatis* respectively using Promega Plant DNA extraction kit. A total of twelve SSR primer pairs were used (Table 3) for molecular study. SSR markers were obtained from Gramene (http://wwwgramene.org/). All SSR PCR amplification reactions were carried out in a total volume 30 μl of which consist 1 x PCR buffer, 1 mM dNTPs, 2 μM SSR primers, 2 mM

| Character | Abbreviations |
|-----------|---------------|
| Vein width (μm) | VW |
| Vein height (μm) | VH |
| Leaf thickness (μm) | LTH |
| Height of mesophyll layer (μm) | MESOH |
| Width of mesophyll layer(μm) | MESOW |
| Bundle cell length(μm) | BCLEN |
| Bundle cell width (μm) | BCWIDT |

Table 2. 
Characters Observed for characterization of wild rice.

| SSR | Chr | Fw5′–3′ | Rev5′–3′ |
|-----|-----|---------|---------|
| RM11 | 7 | tecttcttcccgcgatc | atagcgggagagccttag |
| RM14 | 1 | cccaggagggggagctgg | gtgccaattctcggagaaaa |
| RM19 | 12 | caaaccagagctagacgc | ctaactctgacgcccaaga |
| RM21 | 11 | acagattctcaggggacgg | gtctcatggaggggtcagag |
| RM44 | 8 | agggcctatcgaacaccc | tggggaaactctacctc |
| RM55 | 3 | ctctcggtagtagaggaag | tccgagcttttagaggg |
| RM84 | 1 | tcaaggctcatacctttgat | tgcaaatcgctagtctag |
| RM211 | 2 | cccagagctctcaacaacctg | ttccagaggtctctccc |
| RM219 | 9 | cctcgagtagtgatagagct | catcagctctccct |
| RM253 | 6 | tcctctgatggggcctata | gccaggtagctagag |
| RM280 | 4 | acacagagcactttgcgc | tgggtctgacagcag |
| RM289 | 5 | ttcctgtgcacaacaaacc | ctggcgaactcttcag |

Table 3. 
SSR markers used for the molecular studies.
MgCl\textsubscript{2}, 50 ng of genomic DNA and 0.5 Units of Taq DNA polymerase. SSR alleles were resolved on Poly Acrylamide Gel. The SSR banding patterns were identified using Poly Acrylamide Gel Electrophoresis (PAGE).

2.5 Analysis of Data

Gathered data were analyzed with univariate, bivariate and multivariate statistical procedures. Suitable statistical software was employed in the analysis of data. In addition, data mining analysis were also attempted for the data gathered from the study to reduce the noise in the data set.

Molecular data were analyzed using Genemapper 4.1 software and SSR profiles were analyzed using PowerMarker 3.25.

3. Results

3.1 Morphological studies

The mean values of the parametric morphological measurements of wild rice species are given in Table 4. According to the table, the species *O. rufipogon* indicated highest mean for the plant height (153.23 cm) and the culm length (94.11 cm) and minimum plant height was observed in *O. eichingeri* (99.25 cm). Similarly, the highest leaf length and breadth were found in the samples of *O. nivara* and narrow leaves were occurred in samples of *O. rufipogon*. The variation of ligule length indicated that *O. nivara* possessed a higher ligule length with respect to other species included in the study. The summary of the ANOVA carried out on the parametric lamina morphological characters are shown in Table 5, except ligule length, panicle length, the rest of the characters are significantly varying across the wild rice species.

The association of the non-parametric characters with wild rice species included in the study is shown in Table 6. The characters such as leaf blade pubescent, awn after full heading and intermodal color after full heading are not significantly differ across the species (p > 0.05). However, the rest of the characters are significantly associated with the wild rice species and are of potential characters in separating wild rice species.

| Species | PLHEI (cm) | LBL (cm) | LBW (mm) | LIGULEL (mm) | CULML (cm) | PANICLEL (cm) |
|---------|------------|---------|----------|-------------|------------|-------------|
| Eich    | 99.25      | 41.33   | 10.73    | 9.25        | 90.32      | 22.75       |
|         | 10.84      | 6.50    | 1.20     | 6.15        | 11.11      | 5.97        |
| Niva    | 140.30     | 52.00   | 10.50    | 11.75       | 120.78     | 26.33       |
|         | 10.50      | 6.68    | 0.58     | 1.50        | 21.91      | 2.87        |
| Rhi     | 116.08     | 48.75   | 5.58     | 7.00        | 119.05     | 21.40       |
|         | 3.28       | 2.99    | 1.06     | 3.37        | 1.07       | 0.66        |
| Rufi    | 153.23     | 38.56   | 4.01     | 6.31        | 94.11      | 23.66       |
|         | 7.17       | 6.80    | 4.52     | 6.46        | 14.37      | 2.00        |

Table 4.
Summary of the parametric morphological characters of the four wild rice species (Mean value and standard deviation below mean value).
A total of three clusters were resulted from the cluster analysis of morphological characters (Figure 5) and species were grouped under each cluster with respect to their similarities. The samples of *O. nivara* and *O. rufipogon* were intermingled and separated into two groups. Meanwhile the samples of *O. eichingeri* and *O. rhizomatis* well-separated from 80% similarity level and from rest of the clusters representing two populations. However, one sample of *O. eichingeri* was grouped with *O. rhizomatis*. The phylogenetic tree (Figure 6) constructed by morphological characters clearly showed a well separated cluster of *O. rhizomatis*. The samples of *O. nivara* and *O. rufipogon* were intermingled and separated into four groups. Findings of the study led to conclude that wild rice species in Sri Lanka are “ecological swarms” and represents allopatric or sympatric populations.

| Character | Sum of Squares | df | Mean Square | F   | Sig. |
|-----------|----------------|----|-------------|-----|------|
| PLHEI     | 11727.01       | 3  | 3909.004    | 54.527 | S    |
| LBL       | 647.173        | 3  | 215.724     | 5.522 | S    |
| LBW       | 220.522        | 3  | 73.507      | 7.972 | S    |
| LIGULEL   | 94.823         | 3  | 31.608      | 1.065 | NS   |
| CULML     | 3951.715       | 3  | 1317.238    | 6.74  | S    |
| PANICLEL  | 53.154         | 3  | 17.718      | 1.423 | NS   |

*Note: S = Significant at p < 0.05, NS = Not significant, p > 0.05.

Table 5.

Summary of the ANOVA performed on the parametric morphological characters of the four wild rice species.

| Character | $\chi^2$ Value | df | Sig. |
|-----------|----------------|----|------|
| LBP       |                |    | Constant |
| LBC       | 23.00          | 3  | S    |
| BLC       | 4.97           | 3  | NS   |
| LiguleC   | 23.00          | 3  | S    |
| LiguleS   | 23.00          | 3  | S    |
| CollorC   | 13.55          | 3  | S    |
| AuricleC  | 23.00          | 3  | S    |
| AWNAF   | 12.01          | 6  | NS   |
| AWNC      | 4.55           | 6  | S    |
| ApiculeC  | 7.53           | 6  | S    |
| SeedCC    | 18.59          | 3  | S    |
| LastS     | 39.25          | 12 | S    |
| CULMA     | 22.85          | 6  | S    |
| INCAF     | 7.16           | 6  | NS   |
| CulmS     | 24.28          | 9  | S    |

*Note: S = denote statistically significant difference; NS = Not significant.

Table 6.

Result of $\chi^2$ test performed on the non-parametric morphological characters of the wild rice species included in the study.
3.2 Anatomical studies

The variation of anatomical characters, especially the laminar anatomical features across the wild rice species are given in Table 7. Comparatively, the magnitude of mean values of bundle sheath cell width indicated a considerable variation between the wild rice species *O. eichingeri* (11.77 μm) and *O. rufipogon* (10.74 μm). The summary of the ANOVA (Table 8), indicated that the all the anatomical
The anatomy of the culm and leaf sheath of wild rice species indicated that the characteristic features of the structures reflect the habitat conditions (Figures 7 and 8).

The result of the cluster analysis of anatomical characters of wild rice species is shown in Figure 9. Comparatively, the Dendrogram resulted from the anatomical
features indicated that anatomical characters well-separate the samples of each wild rice species. The samples of *O. rhizomatis* formed a unique group at similarity level of 80%. The pattern of the sample grouping was similar to the results obtained from the cluster analysis of morphological characters. However, samples were homogenized representing each wild rice species by pure tree branch.

The dendrogram resulted from the morphological and anatomical characters are shown in Figure 10. The grouping pattern of wild rice samples obtained from the analysis of morphological characters and anatomical characters reflect the same pattern observed in previously (Figures 5 and 9).

### 3.3 Molecular studies

A total of three clusters were resulted from the cluster analysis of molecular data (Figure 11) and species were grouped under each cluster with respect to
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Figure 10. Dendrogram produced by cluster analysis of morphological and anatomical characters of Wild rice cultivars, O. nivara, O. rufipogan, O. rhizomatis and O. eichingeri.

Figure 11. Dendrogram produced by cluster analysis of molecular data of wild rice species, O. nivara, O. rufipogan and O. rhizomatis.
their genetic similarities. The samples of O. nivara, O. rufipogon and O. rhizomatis were very well separated from 40% similarity level confirming their distant relationship with each other and of independent evolution within Sri Lanka.

4. Discussion

The morphological and anatomical characters were investigated in relation to the species identification and delimitation of wild rice species complex in the country. The results of the morphological characters have indicated that they were useful in identification of wild rice species. However, the ecological resilience of the morphological characters is to be investigated before reaching a firm conclusion on the diagnostic value of the morphological characters. Compared to the morphological characters, the anatomical characters especially, lamina and culm anatomical characters are also indicted higher potential identification of species and delimitation of the wild rice species in each complex. Both morphological and anatomical characters can be used to separate the O. rhizomatis and O. eichingeri (CC) from the rest of wild rice species (AA). Further, based on both morphology and anatomy, O. rhizomatis can be distinguished from O. eichingeri. This finding suggests that species status of these two species deserved to maintain for further confirmation by molecular characterization. As far as the samples of two wild rice species of AA, O. nivara and O. rufipogon is concerned, there were considerable overlaps with respect to morphology and anatomy. However, the analysis of molecular data revealed that samples of O. nivara, O. rufipogon and O. rhizomatis have a distant relationship with each other and undergone independent evolution within Sri Lanka.

Finding of the study led to conclude that wild rice species in the island are “ecological swarms” and represents allopatric or sympatric populations. This finding is further supported by the connotations made by Nelson on the genus Oryza and its species in Sri Lanka [33].

5. Conclusions

The identification of wild rice species, to certain extent, can be made through the morphological and anatomical characters. The delimitation of the species complexes also achieved through the morphology and anatomy specially lamina anatomical characters. The nodal and culm anatomical characters are of limited value in the species identification and delimitation of wild rice species complexes.

However, molecular characterization is more reliable in characterization of wild rice species complexes in Sri Lanka.

The analysis of molecular data revealed that samples of O. nivara, O. rufipogon and O. rhizomatis have a distant relationship with each other and undergone independent evolution within Sri Lanka.

Therefore, studies on the ecological resilience of morphological characters in combination with anatomical and molecular studies are very useful for species enumeration of wild rice complexes in Sri Lanka. The finding led to conclude that wild rice species in Sri Lanka are “ecological swarms” and represents allopatric or sympatric populations.

A comprehensive knowledge on genetic diversity and population structure of wild rice germplasm in Sri Lanka provides useful information to include these
locally adapted and evolved wild rice species in rice crop improvement and breeding programmes.

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References

[1] Fertilizer Levels. https://www.doa.gov.lk/rrdi/index.php?option=com_sppagebuilder&view=page&id=42&lang=en. (Retrieved on 2019.09.06)

[2] Vaughan DA. 1989. The genus Oryza L. current status of taxonomy. IRRI Res. Pap. Ser. 1989; 138:1 europepmc.org › article › agr › ind90027658.

[3] Vaughan DA, Morishima M. BIOSYSTEMATICS of the genus ORYZA. In: Smith CW, Dilday RH, editors. Rice: Origin, History, Technology, and Production. Wiley Series in Crop Science, John Wiley & Sons, Inc., New Jersey; 2002. p. 27–65.

[4] Aggarwal R, Brar D, Khush G. Two new genomes in the Oryza complex identified on the basis of molecular divergence analysis using total genomic NA hybridization. Mol. Gen. Genet. 1997;254:1–12. https://link.springer.com/article/10.1007/s004380050384.

[5] Ge S, Sang T, Lu BR, Hong DY. Phylogeny of rice genomes with emphasis on origins of allotetraploid species. Proc Natl Acad Sci USA. 1999; 96:14400–14405. DOI:10.1073/pnas.96.25.14400.

[6] Chang TT. The origin, evolution, cultivation, dissemination, and diversification of Asian and African rices. Euphytica 1976;25:425–441. https://link.springer.com/article/10.1007/BF00041576.

[7] Sitch LA, Dalmacio RD, Khush GS. Crossability of wild Oryza species and their potential use for improvement of cultivated rice. Rice Genet. Newsl. 1989; 6:58–59. https://shigen.nig.ac.jp/rice/oryzabase/asset/rgn/vol6/v6pS58.html.

[8] Khush GS. Origin, dispersal, cultivation and variation of rice. Plant Mol. Biol. 1997;35: 25–34. https://pubmed.ncbi.nlm.nih.gov/9291957/.

[9] Piegu B, Guyot R, Picault N, Roulin A, Sanijal A, Kim H, Collura K, Brar DS, Jakson S, Wing RA, Panaud O. Doubling genome size without polyploidization: dynamics of retrotransposition-drivengenomic expansions in Oryza australiensis, a wild relative of rice. Genome Res. 2006;16: 1262–1269. http://www.genome.org/cgi/doi/10.1101/gr.5290206.

[10] Nayar NM. Origin and cytogenetics of rice. Advances in Genetics. 1973;17: 153–292. DOI:https://doi.org/10.1016/S0065-2660(08)60172-8.

[11] Oka HI. Origin of cultivated rice. Japan Sci. Soc. Press/Elsevier, Tokyo/Amsterdam; 1988. ISBN 0444989196.

[12] Morishima H, Sano Y, Oka HI. Evolutionary studies in cultivated rice and its wild relatives. Oxford Surveys in Evolutionary Biology. 1992; 8:135–184. https://www.google.com/search?q=Evolutionary+studies+in+cultivated+rice+and+its+wild+relatives.+Oxford+Surveys+in+Evolutionary+Biology.

[13] Ghesquiere A. Evolution of Oryza longistaminata. Rice Genetics Collection Rice Genetics I. 2008. p. 15–25. DOI: 10.1142/9789812814265_0002.

[14] Tateoka T. Taxonomic studies of Oryza II. Several species Complex. Bot. Mag. Tokyo. 1962;75:455–461. www.jstage.jst.go.jp › article › jplantres1887 › _pdf.

[15] Liyanage, ASU, Hemachandra PV, Edimsinghe DK, Seneviratha SK, Takahashi J. Surveying and Mapping of Wild Species of Oryza in Sri Lanka. Jpn. J. Trop. Agr. 2002; 46(1):14–22. DOI: 10.11248/jsta1957.46.14

[16] Abhayagunasekara AVC, Bandaranayake PCG, Samarasinghe WLG, Pushpakumara DKNG. Diversity of wild
rice species in Sri Lanka: some reproductive traits. In: Proceedings of the 7th YSF Symposium, Colombo, Sri Lanka; 2018. P. 7–10. https://www.researchgate.net/publication/326998769_Diversity_of_wild_rice_species_of_Sri_Lankasome_reproductive_traits#fullTextFileContent.

[17] Vaughan DA. A new rhizomatous Oryza species (Poaceae) from Sri Lanka. Botanical Journal of the Linnean Society. 1990;103:159–163. https://doi.org/10.1111/j.1095-8339.1990.tb00182.x

[18] Somaratne S, Weerakoon SR, Siriwardana KGDI. Oryza rhizomatis Vaughan. In. Mondal TK, Henry RI, editors. The Wild Oryza Genomes, Compendium of Plant Genomes. Springer International Publishing AG; 2018. P. 263–269. DOI:10.1007/978-3-319-71997-9_23

[19] Biswal J, Sharma, SD. Taxonomy and phylogeny of Oryza collina. Oryza. 1987;24:24–29. https://agris.fao.org/agris-search/search.do?recordID=IN8800340.

[20] Bor NL. Grasses of Burma, Ceylon, India and Pakistan. Pergamon Press, London; 1960. https://www.cabi.org/isc/abstract/196611602837

[21] Tateoka T. Notes of some grasses. XVI. Embryo structure of the genus Oryza in relation to their systematics. Am J Bot. 1964; 51:539–543. DOI:10.1002/j.1537-2197.1964.tb06667.x

[22] Jena KK, Khush GS. Introggression of genes from Oryza officinalis Well ext Watt. To cultivated rice, O. sativa L. Theoretical and Applied Genetics. 1990; 80:737–745. DOI:10.1007/bf00224186.

[23] Sharma SD, Shastry SVS. Taxonomic studies in genus Oryza L. III. O. rufipogon Griff. sensustricto and O. nivara Sharma et Shastry nom. Nov. Indian Journal of Genetics and Plant Breeding. 1965;25:157–167. grassworld.

m speculated.info > content > taxonomic-studies

[24] Provan J, Corbett G, McNicol JW, Powell W. Chloroplast DNA variability in wild and cultivated rice (Oryza sativa) revealed by polymorphic chloroplast simple sequence repeats. Genome. 1997; 40:104–110. DOI: https://doi.org/10.1139/g97-014.

[25] Wang XK, Cai HW, Cheng KS. The discovery of an Est locus related to the origin, evolution and classification of Asian rice. Chinese Rice Res. Newslt. 1992;7:1–2. www.ricescience.org > abstract > abstract9333.

[26] Dally AM, Second G. Chloroplast DNA diversity in wild and cultivated species of rice (genus Oryza, section Oryza): ladistics-mutation and genetic-distance analysis. Theor. Appl. Genet. 1990;80:209–222. https://link.springer.com/article/10.1007/BF00224389.

[27] Wendel JF, Doyle JJ. Phylogenetic incongruence: Window into genome history and molecular evolution. In. Soltis DE, Soltis PS, Doyle JJ. editors. Molecular Systematics of Plants II: DNA Sequencing. Kluwer, Boston; 1998. p. 265–296. ISBN: 978–0–412-11121-1.

[28] Zou XH, Zhang FM, Zhang JG, Zang LL, Tang L, Wang J, Sang T, Ge S. Analysis of 142 genes resolves the rapid diversification of the rice genus. Genome Biol. 2008;9:R49. http://genomebiology.com/2008/9/3/R49 G.

[29] Bapteste E, Brinkmann H, Lee JA, Moore DV, Sensen CW, Gordon P, Duruflé L, Gaasterland T, Lopez P, Müller M. The analysis of 100 genes supports the grouping of three highly divergent amoebae: Dictyostelium, Entamoeba, and Mastigamoeba. Proc. Natl. Acad. Sci. USA. 2002;99:1414–1419. DOI: 10.1073/pnas.032662799.

[30] Rokas A, Williams BL, King N, Carroll SB. Genome-scale approaches to
resolving incongruence in molecular phylogenies. Nature. 2003; 425:798–804. DOI:10.1038/nature02053.

[31] Cranston KA, Hurwitz B, Ware D, Stein L, Wing RA. Species trees from highly incongruent gene trees in rice. SystBiol. 2009;58:489–500. DOI: 10.1093/sysbio/syp054.

[32] PGRC. Characterization Catalogue of Rice (Oryza sativa). Department of Agriculture., Ministry of Agriculture and Lands, Sri Lanka; 1999.

[33] Harriman NA. (1994). Oryza. In: Flora of Ceylon. Dasanayake MD, Clayton WR, editors. Amerind Publishing Co. Pvt., Ltd., New Delhi, India; 1992. VIII: p. 326–330.