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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. rufipogan* (AA) *O. eichengeri* [CC], *O. rhizomatis* (CC) and *O. granulate* (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 spices 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. rufipogan* (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.
O. rufipogon *(a) panicle (b) growing in a periodically drying temporary ponds.*

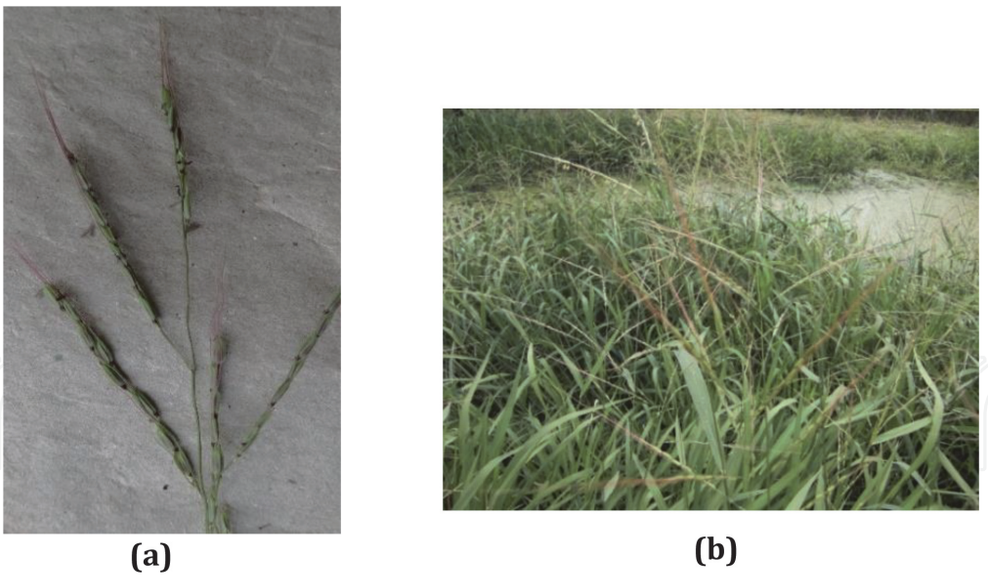

Figure 2.
O. nivara *(a) panicle (b) growing along the border of a canal in Sri Lanka.*

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. offocinalis* 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

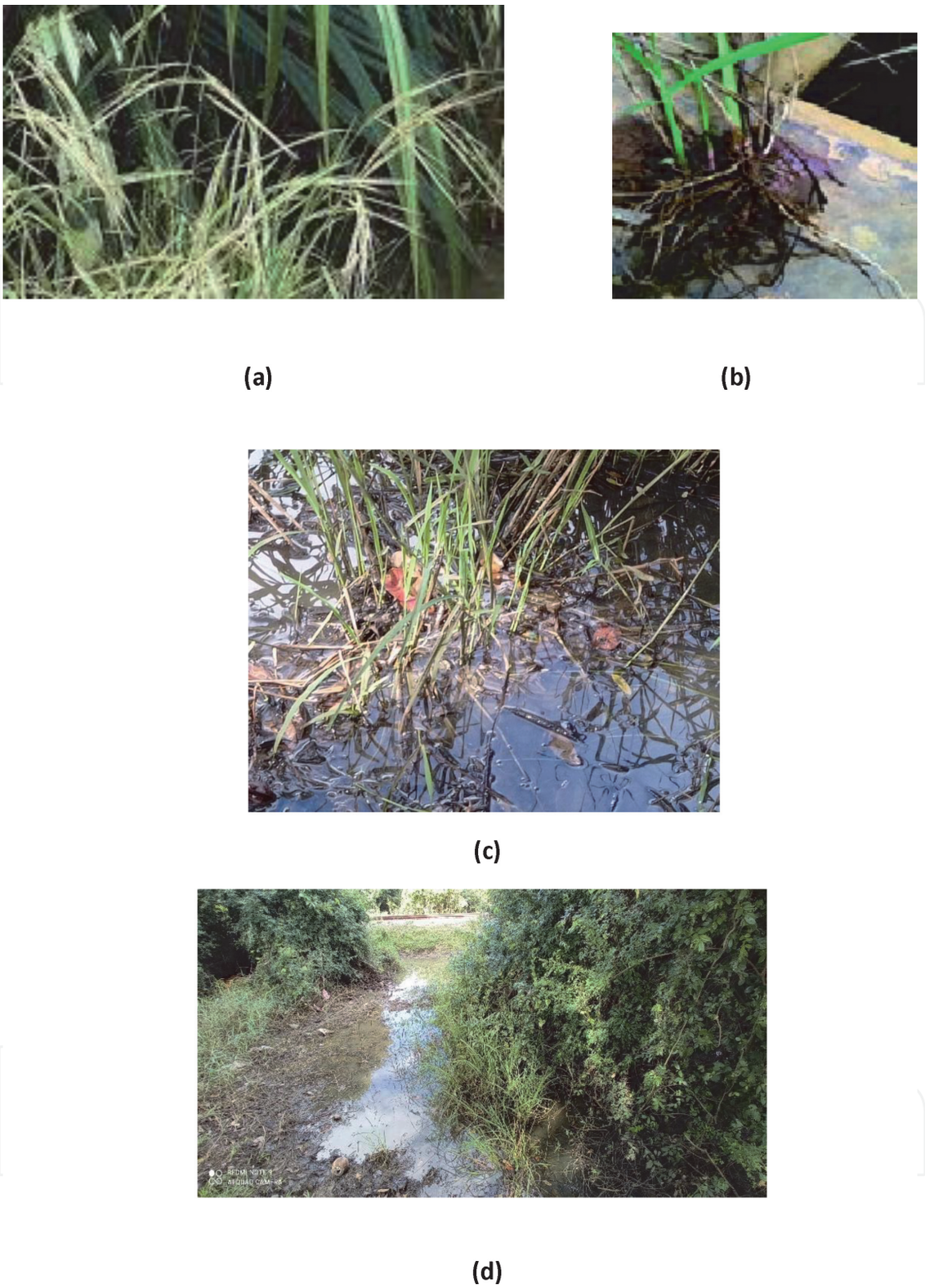

Figure 3.
(a) Panicles (b) Rhizomes (c) well-spread rhizome submerged in water of O. rhizomatis*. (d)* O. rhizomatis *in open spaces in the dry zone (Anuradhapura District), Sri Lanka.*

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 4.
Panicles of O. eichingeri *in open spaces in the forest in the dry zone, 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, Puttlam, 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.

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.

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

Character	Abbreviations
Morphological characters	
Plant Height (cm)	PLH
Leaf blade length (cm)	LBL
Leaf blade wigth (cm)	LBW
Leaf blade pubescence at late vegetative stage	LBP
Leaf blade color at late vegetative stage	LBC
Basal leaf sheath color at late vegetative stage	BLSC
Ligule length at late vegetative stage (cm)	LiguleL
Ligule color at late vegetative stage	LiguleC
Ligule shape at late vegetative stage	LiguleS
collar color at late vegetative stage	CollorC
Auricle color at late vegetative stage	AuricleC
Culm length (cm)	CulmL
Culm angle after flowering	CulmA
Internode color after flowering	IINCAF
Culm strength	CulmS
Panicle length	PanicleL
Panicle type	PanicleT
Panicle excretion	Panicleex
Awning after full heading	AWNAFH
Awn color at maturity	AAWNC
Apiculuscolor	ApiculeC
Seed coat (bran) color at maturity	SeedCC
Leaf senescence	LeafS
Lamina Anatomical characters	
Vein diameter (μm)	VD
Inter Venial distance (μm)	IVD

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.

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://www.gramene.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

SSR	Chr	Fw5′–3′	Rev5′–3′
RM11	7	tctcctcttcccccgatc	atagcgggcgaggcttag
RM14	1	ccgaggagaggagttcgac	gtgccaatttcctcgaaaaa
RM19	12	caaaaacagagcagatgac	ctcaagatggacgccaaga
RM21	11	acagtattccgtaggcacgg	gctccatgagggtggtagag
RM44	8	acgggcaatccgaacaacc	tcgggaaaacctaccctacc
RM55	3	ccgtcgccgtagtagagaag	tcccggttattttaaggcg
RM84	1	taagggtccatccacaagatg	tgcaaatgcagctagagtac
RM211	2	ccgatctcatcaaccaactg	cttcacgaggatctcaaagg
RM219	9	cgtcggatgatgtaaagcct	catatcggcattcgcctg
RM253	6	tccttcaagagtgcaaaacc	gcattgtcatgtcgaagcc
RM280	4	acacgatccactttgcgc	tgtgtcttgagcagccagg
RM289	5	ttccatggcacacaagcc	ctgtgcacgaacttccaaag

Table 3.
SSR markers used for the molecular studies.

$MgCl_2$, 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).

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	χ^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
AWNAFH	13.01	6	NS
AWNC	4.55	6	S
ApiculeC	7.53	6	S
SeedCC	18.59	3	S
LasfS	39.25	12	S
CULMA	22.85	6	S
INCAF	7.16	6	NS
CulmS	24.28	9	S
Panilceexer	Constant		

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

Table 6.
Result of χ^2 test performed on the non-parametric morphological characters of the wild rice species included in the study.

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. rhizamatis*. 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.

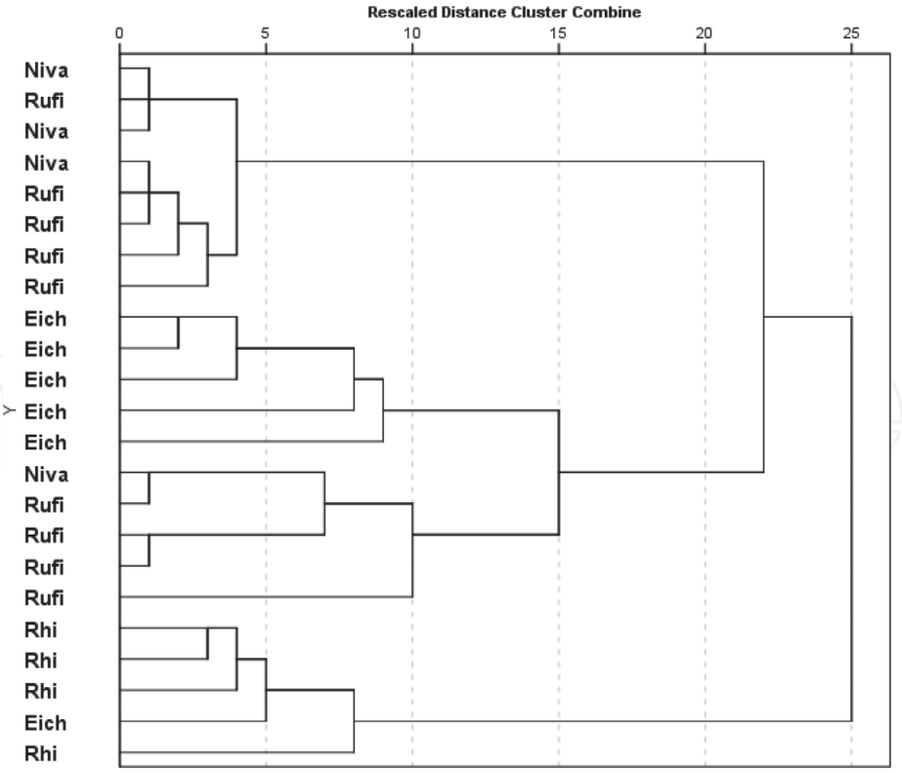

Figure 5.
Dendrogram produced by cluster analysis of 22 morphological characters of wild rice species, O. nivara, O. rufipogan, O. rhizomatis *and* O. eichingeri.

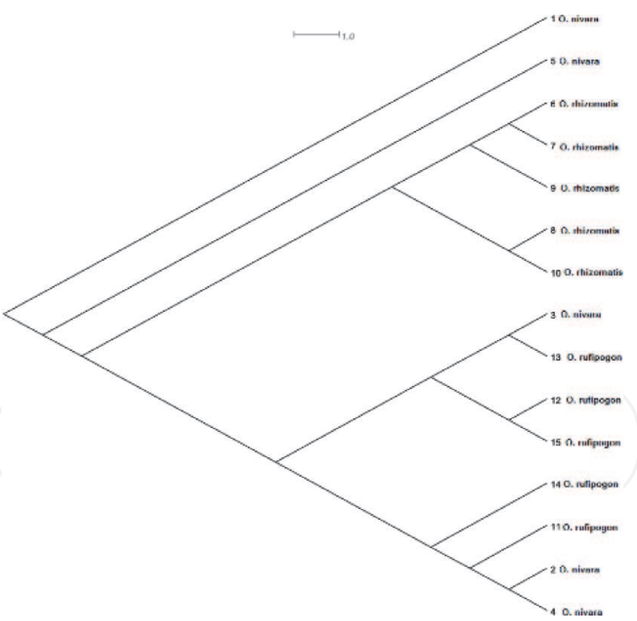

Figure 6.
Phylogenetic Tree constructed by 22 morphological characters of wild rice species, O. nivara, O. rufipogan, O. rhizomatis.

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

Species	VD	IVD	VW	VH	LTH	MESOH	MESOW	BCLEN	BCWIDT
Eich	6.15	181.48	20.78	24.32	75.72	12.62	6.75	11.78	11.77
	0.80	11.79	1.53	2.76	4.43	0.70	1.88	0.95	1.70
Niva	4.33	207.08	29.65	37.03	87.68	12.33	7.65	10.18	9.85
	0.25	6.37	2.99	6.82	5.28	1.31	1.04	0.79	0.58
Rhi	5.65	155.53	25.00	28.48	68.60	12.10	3.63	10.55	8.55
	0.82	1.32	1.07	1.14	5.80	0.62	0.93	0.91	1.05
Rufi	4.91	210.90	28.91	34.41	85.68	12.49	7.97	11.32	10.74
	0.45	6.82	2.15	5.59	5.93	0.83	0.92	1.46	1.15

Table 7.
Summary of the parametric lamina anatomical characters of the wild rice species (Mean value and standard deviation below mean value).

Character	Sum of Squares	df	Mean Square	F	Sig.
VD	9.953	3	3.318	8.978	S
IVD	10089.31	3	3363.102	53.518	S
VW	295.528	3	98.509	23.708	S
VH	542.508	3	180.836	7.955	S
LLTH	1150.885	3	383.628	12.917	S
MESOH	0.72	3	0.24	0.319	NS
MESOW	55.442	3	18.481	11.584	S
BCLEN	7.877	3	2.626	1.914	NS
BCWIDT	27.049	3	9.016	5.856	S

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

Table 8.
Summary of the ANOVA performed on the laminar anatomical characters of the four wild rice species.

characters except mesophyll height and bundle sheath height. 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

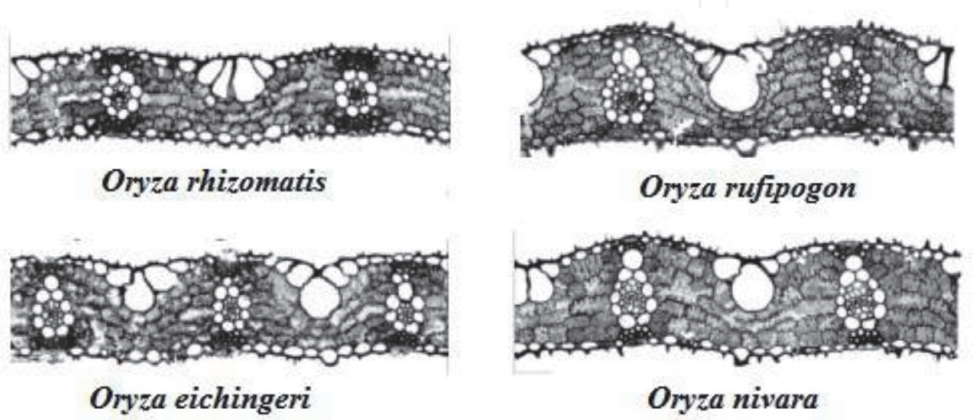

Figure 7.
Laminar anatomical characters of 4 wild rice species collected during the study.

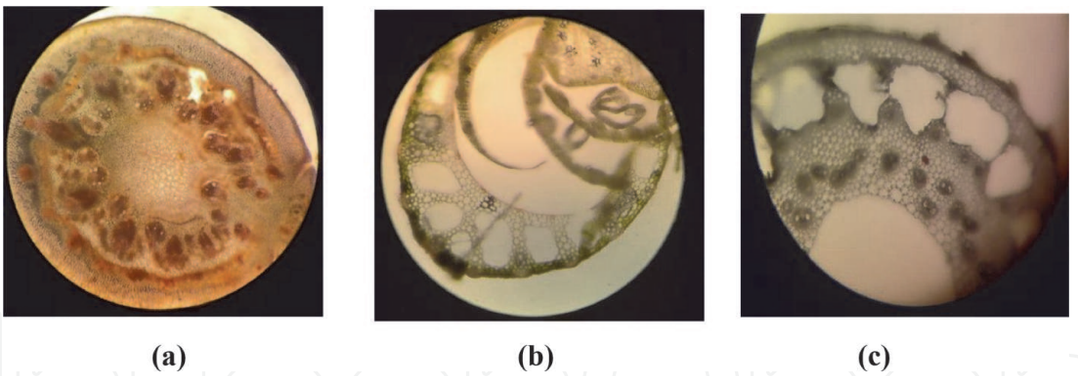

Figure 8.
(a) The transverse section of culm of O. rhizomatis *(b) the section through a portion of* O. rufipogon *culm encircled by leaf sheath (c) the culm section of* O. nivara.

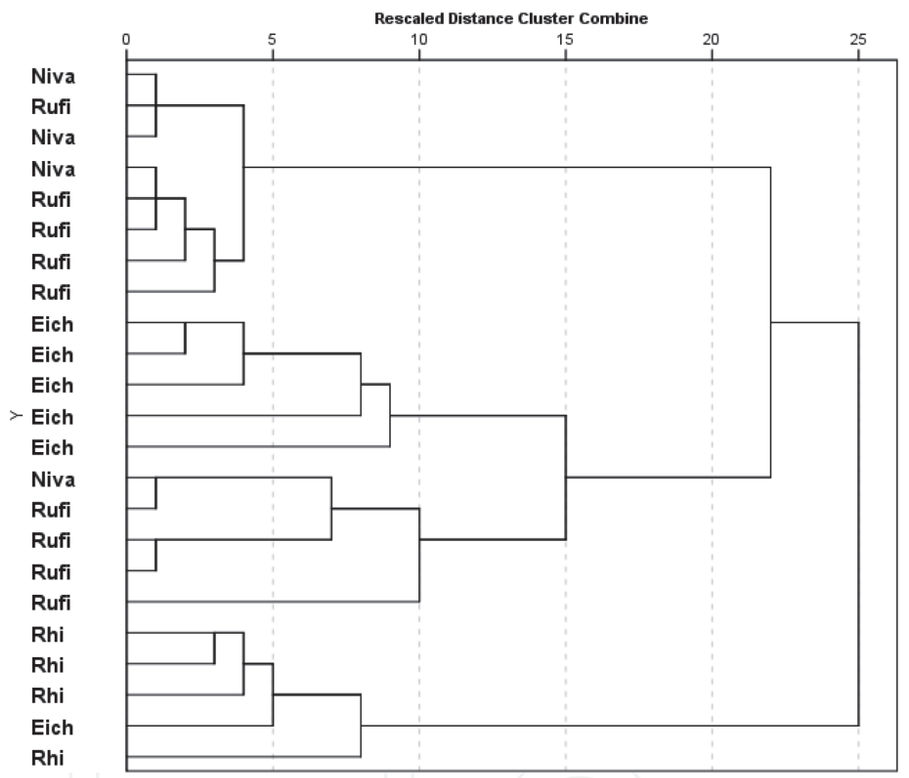

Figure 9.
Dendrogram produced by cluster analysis of anatomical characters of wild rice species, O. nivara, O. rufipogan, O. rhizomatis *and* O. eichingeri.

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

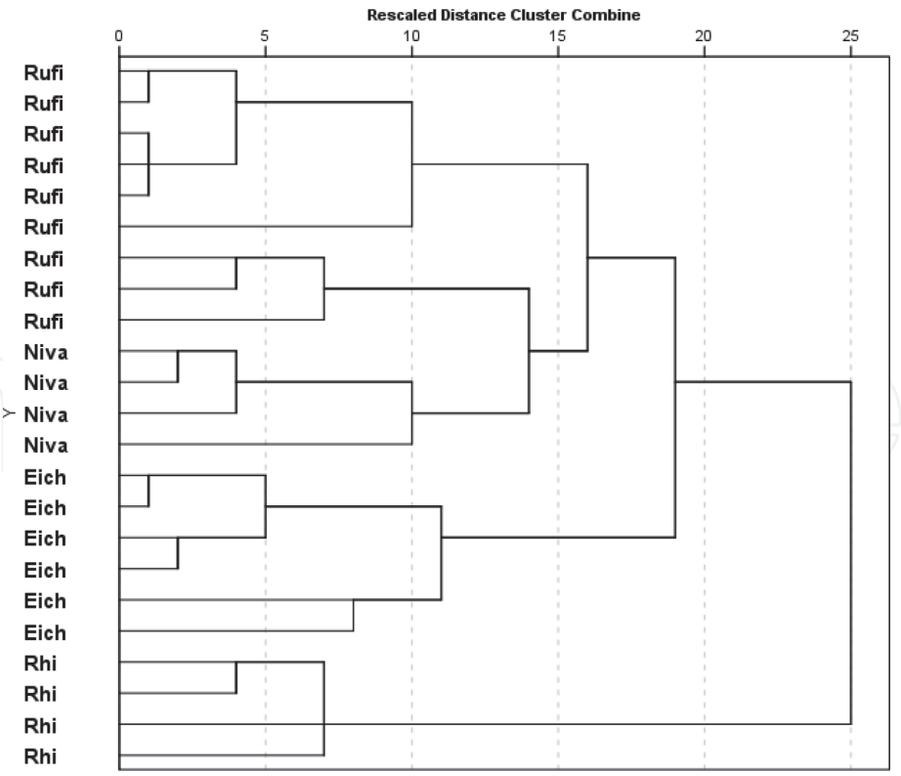

Figure 10.
Dendrogram produced by cluster analysis of morphological and anatomical characters of Wild rice cultivars, O. nivara*,* O. rufipogan*,* O. rhizomatis *and* O. eichingeri*.*

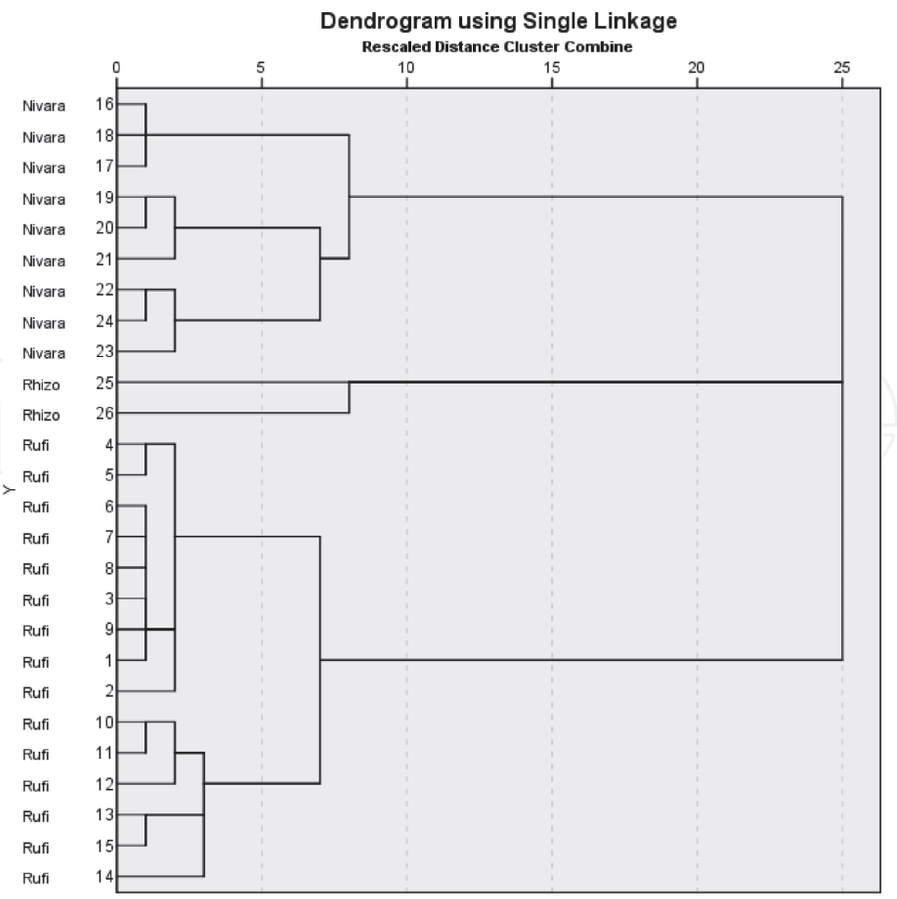

Figure 11.
Dendrogram produced by cluster analysis of molecular data of wild rice species, O. nivara*,* O. rufipogan *and* O. rhizomatis*.*

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 overleaps 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 adapled and evolved wild rice species in rice crop improvement and breeding programmes.

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