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Phenotypic Characterization of *Oryza nivara* (Sharma *et* Shastry) Collected from Different Ecological Niches of Sri Lanka

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ABSTRACT

Information on the genetic diversity of wild rice species in Sri Lanka is relatively meagre, though it plays a key role in crop improvement programs of cultivated rice (*Oryza sativa* L.). The present study was carried out to identify the morphological variation pattern of the wild populations of *O. nivara* in Sri Lanka. Seven populations (P1 to P7) collected from different agro-ecological regions were characterized in a common garden based on nine morphological traits. The findings revealed a high level of phenotypic variation between populations when compared to within a population. The most variable traits were the flag leaf panicle neck length (FLPNL) and flag leaf angle (FLA), whereas the least variable trait was the flag leaf length (FLL). Box plots clearly illustrated the large differentiation of phenotypic traits in the entire distribution of wild rice populations. The cumulative values of the two principal components, i.e., FLPNL and FLA, explained 58.7% of the total variance. Populations from similar natural habitats clustered together. The P7 was adapted to intercept more sunlight by increasing flag leaf width (FLW) and FLA to compete with weeds and other shrubs. P2 and P5 were the most closely related populations representing approximately similar ecological conditions of the dry zone. The P3 population from the intermediate zone showed a vigorous plant growth with the highest plant height, culm girth and awn length ($P < 0.05$). Knowledge of such morphological diversity would facilitate designing conservation strategies and basic information for the proper utilization of wild resources in rice genetic improvement.

KEYWORDS

AA-genome; morphological traits; natural habitats; population differentiation; wild rice

1 Introduction

Rice (*O. sativa* L.) is the staple food for more than one-third of the world's population and the most important crop cultivated in Asia. The genetic diversity of cultivated rice has rapidly narrowed down after the green revolution due to the development of high-yielding cultivars focusing on a few agronomic traits [1–3]. Rice improvement efforts have thus been directed towards incorporating biotic and abiotic resistance to the cultivars and the physiological processes governing yield potential to optimize growth duration and improve grain quality of the cultivars [4,5]. The wide range of genetic diversity in *Oryza* species has been well documented [6–10]. In particular, the wild species closely related to cultivated rice have a valuable gene pool and play a pivotal role in rice breeding programs by contributing genes resistant to biotic stresses and tolerance to abiotic stresses [2,5,11]. The species of the genus *Oryza* are widely diverse morphologically [12–16] and are genetically represented by distinct genome types, which provide a valuable opportunity to investigate variations of rice breeding programs [13,17]. Due to their high genetic compatibility with cultivated rice, species possessing the AA-genome are the most accessible genetic resources among the wild relatives [18]. Therefore, the transfer of alien genes from such wild relatives is readily accomplished via sexual hybridization [19]. The development of resistance for biotic stresses such as grassy stunt virus [20], bacterial blight [21], rice blast [22], sheath blight [22], green rice leafhopper [5] are such successful applications that have been achieved using the wild species, *Oryza nivara* (Sharma *et* Shastry). Moreover, *O. nivara* has shown varying degrees of resistance to the brown planthopper (BPH; *Nilaparvata lugens* Stal.) [23,24], indicating the availability of varying degrees of genetic diversity in terms of BPH resistance. Furthermore, *O. nivara* has unique traits that could be used in rice breeding, such as high micronutrient content [25] and the unique yield traits, namely, kernel characteristics [26], panicle length [27], seed weight [26], seed characteristics [28], grain yield [27,29,30], number of tillers [25] and number of panicles per plant [31].

Furthermore, *O. nivara* and *Oryza rufipogon* (Griff) are the progenitors of Asian cultivated rice. They have been recognized as valuable genetic sources for rice genetic improvement programs [5]. *O. rufipogon* is a perennial cross-pollinator found in permanently wet areas such as ponds and swamps, while *O. nivara* is a wild, annual diploid species of Asian origin carring the AA genome. These two species can readily hybridize with cultivated rice. *Oryza nivara* is the most closely related to *O. sativa* in terms of phenotypic and life-history traits and probably the direct progenitor of Asian rice [32,33]. Both species showed allopatric distribution in Sri Lanka, enhancing the potential of sharing genes with cultivated rice [34–36]. The annual *O. nivara* is globally distributed in the tropics and subtropics of Asia [13] and Southern and Southeast Asia [32,33]. However, *O. nivara* found in South Asia is morphologically more differentiated than mainland Asia [37].

In Sri Lanka, *O. nivara* was first reported in 1963 in the Trincomalee district of the eastern province [38]. The species is widely distributed but mostly confined to the dry zone and marginally extending to the intermediate zone of the country [34,35,39]. The size, morphology, and geographic distribution of the natural populations of this species vary considerably. A high level of phenotypic variations of *O. nivara* populations across the geographic locations in Sri Lanka has been recorded [40]. Though the habitat preference of *O. nivara* is shallow water, some populations exist in habitats with water levels nearly 1 m in depth during the rainy season (*in-situ* life cycle observation). Flowering times of wild populations also vary from place to place, with the peak of flowering time from January to May [41]. *Oryza nivara* populations had previously been reported in nine out of 25 districts in Sri Lanka [42], but current field investigations showed that the geographic range of the species has decreased. The existing populations have shrunk due to habitat loss and degradation caused by agriculture and urbanization [39]. Therefore, a better understanding of the genetic diversity of *O. nivara* is instructive both for developing the conservation management for germplasm collection, and effective utilization of genetic resources in rice improvement programs in Sri Lanka.

In the present study, we conducted a baseline study on the *O. nivara* populations in Sri Lanka to identify the population diversity across the country based on selected morphological traits. Regardless of rapid changes in the climate, *O. nivara* populations across the country have adapted well, displaying robust and

diverse morphological traits to their native habitat. Thus, utilizing the diversity of wild rice, *O. nivara*, is critical for developing new cultivars that they respond to future climate threats. Consequently, the development of "climate-ready rice" varieties is essential as they will provide significant benefits to farmers in developing countries. Thus, our study focused the ability of *O. nivara* to adapt to rapid changes in local climate through morphological changes, providing new insights for future research on speciation and local adaptation.

2 Materials and Methods

2.1 Sample Collection and Morphological Characterization

Based on GPS coordinates available from the earlier reports [34], seven wild populations (P1 to P7) of *O. nivara* were collected from an intermediate and a dry zone (Fig. 1), exhibiting a broad range of typical environments [39]. The typical *O. nivara* populations were identified based on several distinctive features, including panicle type, culm type and length, and anther length. Thirty individuals were randomly collected from each population with a minimum distance of five meters between any two individuals. (Fig. 1, Table 1). The selected plants were carefully uprooted with an intact soil mass of 15 cm radius and 15 cm deep and planted in cement pots filled with topsoil in a common garden at the Faculty of Agriculture, University of Ruhuna in Sri Lanka 06.08°N, 80.56°E). The established plants were allowed to grow for two consecutive years (2016–2017). A fertilizer mixture containing Urea: Triple Super Phosphate: Muriate of Potash to provide a N:P:K ratio of 4:1:1 was applied at a rate of 2.0 g per plant per month to support the plant growth during the study period. The nine quantitative parameters were measured as defined by the Africa Rice Center and the Biodiversity International, International Rice Research Institute (IRRI) [43]. All the observations and measurements were taken by the following methods described in the rice descriptors [44].
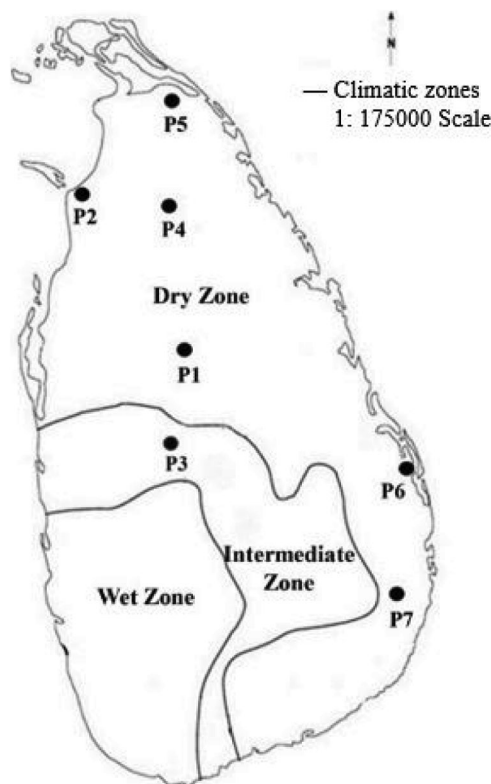

Figure 1: The distribution of the seven *O. nivara* populations sampled from intermediate and dry zones of Sri Lanka

Table 1: Information on habitat and location for the seven populations of *O. nivara* used in the study

Population code	Specific location	Latitude	Longitude	Habitat	Mean annual T° (°C))	Rain fall (mm)	Soil type
P1	Maradankadawala, Anuradhapura	08°07'44.95"	80°33'46.87"	Road reservation	29	>900	Reddish Brown Earth, Low Humic Gley
P2	Sirnavetkulum, Mannar Rd, Mannar	08°54'36.40"	79°57'42.30"	Road reservation	31	>750	Solodized, Solonets, Solonchacks & Grumusol
P3	Rideegama, Kurunegala	07°33'24.88"	80°29'41.96"	Road, deepwater field	27.2	>1400	Red Yellow Podsolic, Low Humic Gley, Reddish Brown Latosol, Regosol
P4	105 km post, A-9 Rd, Vavuniya	08°51'06.00"	80°29'06.04"	Road reservation	27.4	>900	Reddish Brown Earth, Low Humic Gley
P5	Paranthan-Mullaitivu Rd, Kilinochchi	09°25'55.20"	80°29'56.50"	Road reservation, footpath	30	>800	Red Yellow Latosol, Regosol
P6	Vellavelly, Batticaloa	07°30'33.10"	81°43'55.10"	Shallow water lake	27.4	>1100	Reddish Brown Earth, Old alluvial, Low Humic Gley, Regosol & Bolodized-Solonet
P7	Lahugala Rd, Siyambalanduwa	06°53'48.80"	81°41'22.90"	Forest area	26.3	>900	Reddish Brown Earth, Low Humic Gley

Note: Morphological data collected included the plant height (P-H), culm girth (C-G), flag leaf length (FL-L), flag leaf width (FL-W), flag leaf angle (FL-A), flag leaf panicle neck length (FL-PN-L), plant spreading angle (PS-A), awn length (AW-L) and panicle neck spikelet length (PN-SP-L).

2.2 Data Analysis

All the analysis were carried out using Minitab 17 and SAS 9.1 statistical packages. Each parameter was subjected to an analysis of variance to discover particular traits that differed significantly among populations. Pearson's correlation analysis was conducted on quantitative variables. Populations were clustered by performing cluster analysis (Dendrogram by cluster variable option of centroid linkage method) and PCA analysis where populations were grouped according to the first two principal components (biplot analysis).

3 Results

3.1 Identification of Adaptive Morphological Traits

The morphological differences among populations were studied to identify the significant traits involved in population differentiation. The ANOVA showed that P-H ($P < 0.0001$), C-G ($P < 0.0001$), FL-L ($P < 0.0001$), FL-W ($P < 0.0001$), FL-A ($P < 0.0001$), AW-L ($P < 0.0001$), FL-PN-L ($P < 0.0001$), PS-A ($P < 0.0001$) and PN-SP-L ($P < 0.0001$) were significantly different among the populations (Table 2). A high

level of variance was observed among populations for the tested quantitative traits. Pooled means of traits calculated by considering all population individuals are presented in Table 2.

Table 2: Comparison of morphological traits among seven populations collected from Sri Lanka

Character*	Population							Pooled mean	Pooled SD	Pooled SE
	P1	P2	P3	P4	P5	P6	P7			
P-H (cm)	96.8^b	81.1^{de}	114.8^a	97.8^b	83.2^d	70.8^e	86.1^c	90.7	2.858	1.080
C-G (cm)	1.7^b	1.6^c	1.9^a	1.6^c	1.3^e	1.4^d	1.2^f	1.5	0.040	0.015
FL-L (cm)	20^b	18.3^c	20.7^b	20.1^b	20.1^b	22.2^a	17.6^c	19.8	1.264	0.478
FL-W (mm)	9.3^b	7.0^f	8.7^d	7.2^e	9.0^c	6.9^f	10.0^a	8	0.317	0.120
FL-A (º)	74.39^b	40.3^c	41.73^c	30.65^d	40.24^c	34.13^d	100.47^a	52.9	6.412	2.424
FL-PN-L (cm)	7.8^a	1.5^e	2.3^c	1.3^f	1.0^g	5.4^b	1.6^d	2.7	0.341	0.129
PS-A (º)	37.23^b	30.48^e	14.66^g	39.65^a	28.71^f	30.56^d	32.27^c	31.1	1.088	0.411
AW-L (cm)	6.1^d	6.3^{cd}	8.6^a	8.0^b	6.5^c	3.3^f	5.5^e	6.3	0.365	0.138
PN-SP-L (cm)	1.2^f	2.0^c	1.8^e	1.0^g	1.9^d	2.3^a	2.2^b	1.8	0.072	0.027

Note: P-H; plant height, C-G; culm girth, FL-L; flag leaf length, FL-W; flag leaf width, FL-A; flag leaf angle, FL-PN-L; flag leaf panicle neck length, PS-A; plant spreading angle, AW-L; awn length and PN-SP-L; panicle neck spikelet length. Within a row, means followed by the same letters are not significantly different by Duncan's Multiple Range Test (DMRT) at $P > 0.05$.

The highest P-H observed in the P3 population ($P < 0.05$) belonged to the intermediate zone. The P-H of P6 was the shortest (38% lower than the P3), which showed statistically similar results to those of P2 ($P > 0.05$). The P3 showed the highest C-G, which was 58% higher than that of P7, which recorded the lowest C-G ($P < 0.05$).

The plants in P6 had the longest FL-L ($P < 0.05$), while the P2 and P7 populations had no significant difference in lengths ($P > 0.05$) but the lowest FL-L. However, P7 had the highest FL-W ($P < 0.05$), which was 45% higher than the plant populations with the lowest FL-W (P2 and P6). The P7 population had the highest FL-A ($P < 0.05$), while the P4 and P6 populations had the lowest FL-A.

Plants in P1 recorded the highest FL-PN-L, while those in P5 recorded the lowest. The PS-A was the highest in P4 and the lowest in P3. The P3 population showed the highest AW-L, which was 260% higher than that in P6 ($P < 0.05$), which showed the lowest AW-L. The highest PN-SP-L was recorded from plants in P6, while the lowest was from those in the P4 population. All populations showed a significant difference ($P < 0.05$) in the parameters FL-PN-L, PS-A and PN-SP-L.

3.2 Within and among Population Diversity of Growth Characteristics
Variations of each parameter were demonstrated within and among populations (Table 3). Some traits revealed greater population variability leading to a high coefficient of variation (CV) in FL-PN-L (86.79%) followed by FL-A with 49.98%. In contrast, some traits such as FL-L, P-H, FL-W, and C-G showed a comparatively lower CV (7–15%) and those of PS-A, AW-L and PN-SP-L were moderate between 25-30%. Trait-specific variability patterns were found within populations. Similarly, C-G of P7, FL-A of P2, P4, P6 and P7, FL-PN-L in P3, P4, P5, P6 and P7, AW-L in P6 and PN-SP-L of P4 all exhibited a significant variance within the populations.

Table 3: The standard deviation of morphological characteristics within and among populations

Traits	Within population							Among population
	P1	P2	P3	P4	P5	P6	P7	
P-H	1.477	2.805	0.489	1.915	3.771	2.721	4.028	12.605
	(1.53)	(3.46)	(0.43)	(1.96)	(4.53)	(3.41)	(4.68)	(13.80)
C-G	0.008	0.055	0.034	0.020	0.048	0.018	0.057	0.233
	(0.46)	(3.34)	(1.83)	(1.21)	(3.57)	(1.30)	(4.68)	(15.06)
FL-L	1.578	0.597	0.970	0.772	1.400	2.107	0.859	1.504
	(7.88)	(3.26)	(4.70)	(3.85)	(6.97)	(9.50)	(4.88)	(7.57)
FL-W	0.47	0.32	0.30	0.26	0.33	0.35	0.21	1.18
	(4.99)	(4.56)	(3.54)	(3.49)	(3.78)	(5.18)	(2.14)	(14.36)
FL-A	1.987	4.742	2.392	3.132	1.925	3.589	13.348	25.838
	(2.67)	(11.77)	(5.73)	(10.22)	(4.78)	(10.51)	(13.29)	(49.98)
FL-PN-L	0.161	0.054	0.463	0.225	0.194	0.681	0.233	2.583
	(2.07)	(3.58)	(19.90)	(17.84)	(19.30)	(12.71)	(14.73)	(86.79)
PS-A	1.532	2.150	0.970	0.313	0.676	0.455	0.964	8.022
	(4.11)	(7.05)	(6.62)	(0.79)	(2.35)	(1.49)	(2.99)	(26.30)
AW-L	0.094	0.122	0.290	0.475	0.268	0.629	0.289	1.728
	(1.55)	(1.93)	(3.37)	(5.93)	(4.14)	(18.96)	(5.29)	(27.32)
PN-SP-L	0.049	0.030	0.050	0.096	0.103	0.057	0.063	0.517
	(4.21)	(1.49)	(2.82)	(10.03)	(5.41)	(2.45)	(2.82)	(29.39)

Note: P-H; plant height, C-G; culm girth, FL-L; flag leaf length, FL-W; flag leaf width, FL-A; flag leaf angle, FL-PN-L; flag leaf panicle neck length, PS-A; plant spreading angle, AW-L; awn length and PN-SP-L; panicle neck spikelet length. Values presented within parenthesis are coefficient of variation (CV%).

The boxplots simply demonstrated the overall patterns of the entire population distribution regarding the measured parameters and provided a simple method to show the variance of nine morphological characteristics among populations (Fig. 2).

3.3 Relationship Among Morphological Traits

Correlations between parameters evaluated using the Pearson correlation matrix revealed that most of the relationships were statistically significant ($P < 0.05$; Table 4). The P-H with C-G and AW-L, and FL-A with FL-W, showed a strong positive correlation ($r > 0.7$), while PN-SP-L with C-G and AW-L showed a strong negative correlation ($r > 0.6$).

Identification of the genetically closely related populations is critical for the conservation and use of *O. nivara* populations and their natural habitats. The dendrogram illustrated in Fig. 3 was created using a hierarchical cluster analysis based on morphological variation patterns. Populations designated to one cluster had mostly comparable morphological traits that permitted them to be separated from the rest. Results indicated that four of the seven major clusters showed a similarity value of 99.22 and were the most closely associated populations with strong identification (Fig. 3). Furthermore, the P2 and P5 populations formed the first cluster (similarity level = 99.75). The first cluster with P1 and

P4 populations was considered as the first cluster group. The P6 and P3 populations made up the second and third clusters, respectively. Population P7 did not cluster with others indicating the highest morphological difference to the rest.
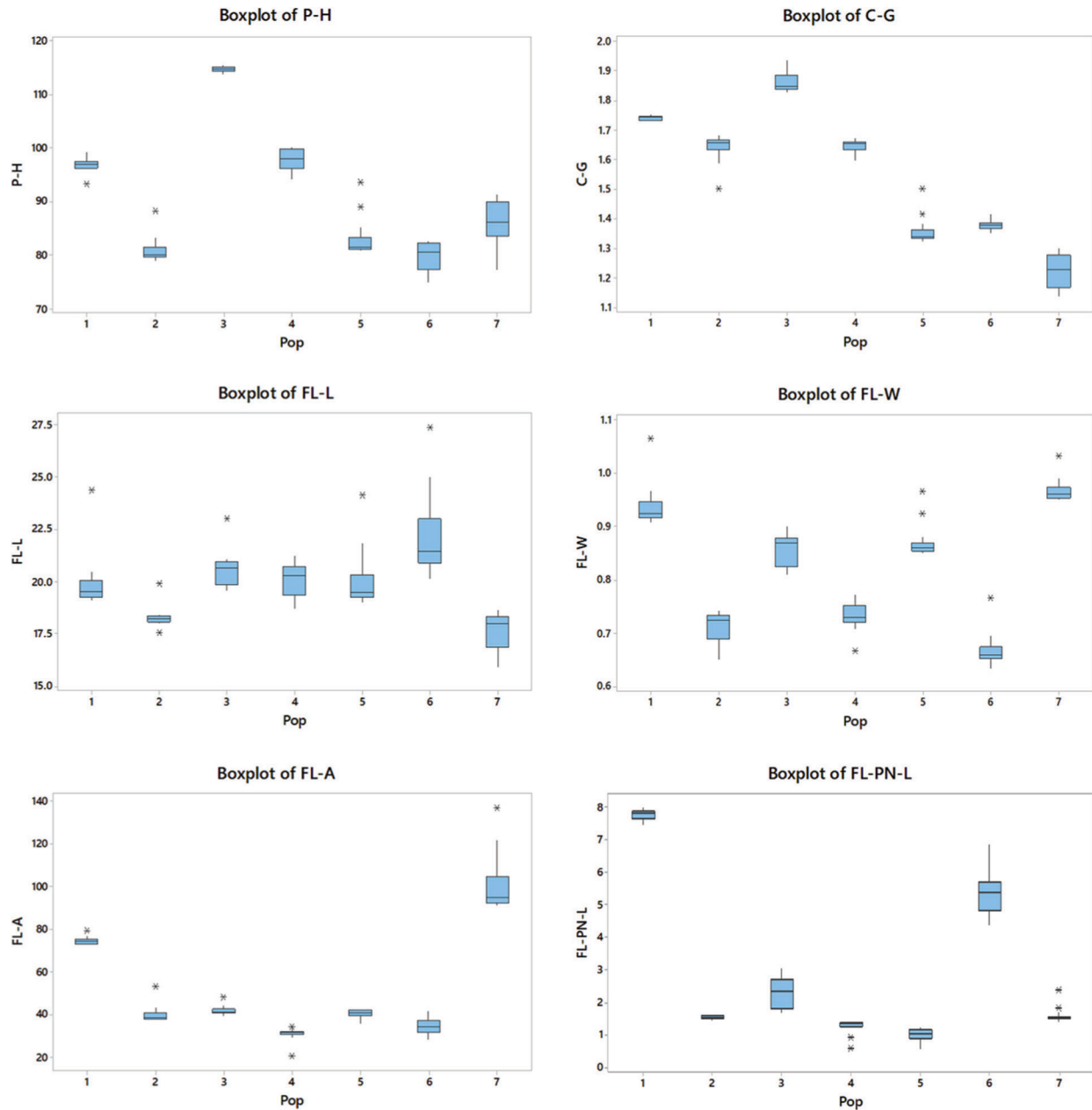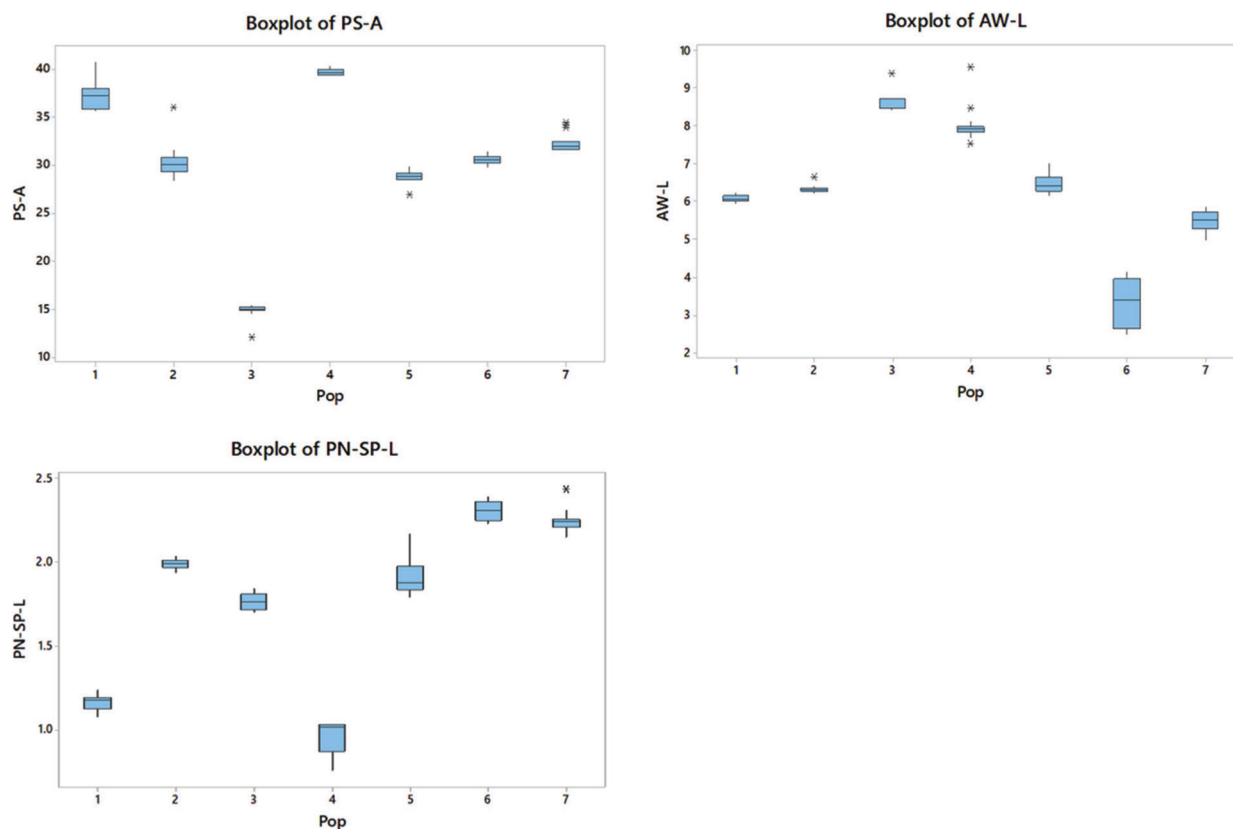

Figure 2: (Continued)

Figure 2: P-H; plant height, C-G; culm girth, FL-L; flag leaf length, FL-W; flag leaf width, FL-A; flag leaf angle, FL-PN-L; flag leaf panicle neck length, PS-A; plant spreading angle, AW-L; awn length and PN-SP-L; panicle neck spikelet length. Outliers are indicated with a star (*). The size of each boxplot indicates the extent of variation in each population in respect of each trait. The upper and lower horizontal lines show the IQR range

Table 4: Pearson correlation matrix for morphological characteristics of *O. nivara*

Trait	P-H	C-G	FL-L	FL-W	FL-A	FL-PN-L	PS-A	AW-L	PN-SP-L
P-H	1.0000								
C-G	0.7057*	1.0000							
FL-L	0.1686	0.2704*	1.0000						
FL-W	0.1282	−0.3805*	−0.2294*	1.0000					
FL-A	−0.1005	−0.4678*	−0.5514*	0.7472*	1.0000				
FL-PN-L	0.0318	0.2186*	0.3706*	−0.0148	0.1180	1.0000			
PS-A	−0.3458*	−0.1833	−0.1264	−0.1406	0.1221	0.1514	1.0000		
AW-L	0.7604*	0.6080*	−0.1365	0.0345	−0.2413*	−0.4597*	−0.1825	1.0000	
PN-SP-L	−0.5261*	−0.6036*	−0.0794	0.1742	0.2862*	−0.1007	−0.4630*	−0.6331*	1.0000

Note: P-H; plant height, C-G; culm girth, FL-L; flag leaf length, FL-W; flag leaf width, FL-A; flag leaf angle, FL-PN-L; flag leaf panicle neck length, PS-A; plant spreading angle, AW-L; awn length and PN-SP-L; panicle neck spikelet length. Note: * marked significant correlations.
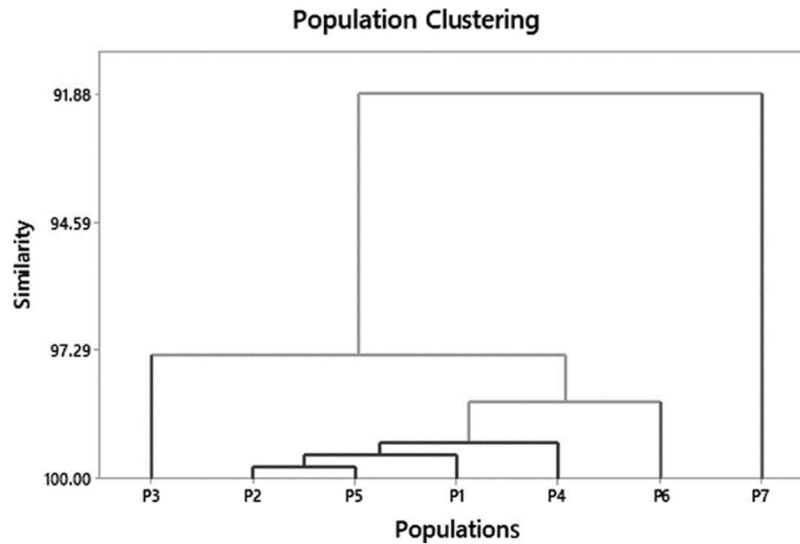
Figure 3: The morphological relationship among the seven *O. nivara* populations in Sri Lanka

3.4 Grouping of Individuals in Each Population Based on Principal Component Analysis

The results revealed that the cumulative values of the first two principal components explained 58.7% of the total variance (Table 5). The PC1 and PC2 explained 35.7% and 23% of the total variance, respectively. Certain morphological traits of *O. nivara* populations contributed to group the population parallel to their existing environments. Biplot analysis illustrated the population grouping based on morphological traits was shown in Fig. 4. For example, P7 recorded a relatively higher FL-A and differed with other populations, which was confirmed from the cluster analysis.

Table 5: First three principal components showing the contribution of all quantitative traits to total morphological variation and proportion of the variance

Characters	Principal component		
	1	2	3
P-H	−0.453	−0.275	0.018
C-G	−0.505	0.013	0.098
FL-L	−0.184	0.456	0.036
FL-W	0.134	−0.546	0.187
FL-A	0.325	−0.476	0.271
FL-PN-L	0.009	0.24	0.569
PS-A	0.093	0.096	0.593
AW-L	−0.448	−0.347	−0.152
PN-SP-L	0.415	0.066	−0.427
Proportion	35.7%	23.0%	16.6%

Note: P-H; plant height, C-G; culm girth, FL-L; flag leaf length, FL-W; flag leaf width, FL-A; flag leaf angle, FL-PN-L; flag leaf panicle neck length, PS-A; plant spreading angle, AW-L; awn length and PN-SP-L; panicle neck spikelet length.
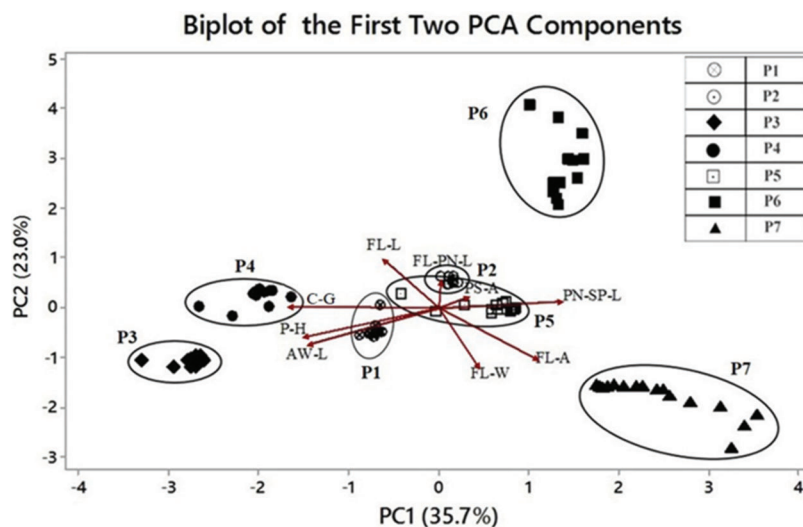
Figure 4: Biplot cluster against the principal component analysis (PC1 on the X-axis and PC2 on the Y-axis). Determination of closely related individuals within and among populations illustrates an overall picture of the variation pattern of *O. nivara* found in different geographical regions of Sri Lanka

Biplot also showed that some populations are separated clearly while some are overlapped (Fig. 4). The results indicated that P2 and P5 had been grouped as they are strongly associated with their natural habitats. It also further confirmed the results of PCA. Population P7 showed distinct population differentiation from other *O. nivara* populations based on a different level of variation of plant traits.

4 Discussion

4.1 Phenotypic Variation within and among O. nivara Populations in Sri Lanka

Earth's average temperature is anticipated to rise from 2 to 4.5°C in the twenty-first century [45] if no climate actions are implemented globally. The frequency of stress spells, their effect on daily life, and damage to agricultural crops are used to evaluate the impact of climate change and environmental variation, which will eventually disrupt the ecosystem [46]. The changing pattern of climatic factors, specifically rainfall and temperature, are primary sources affecting crop yields, thus making, developing countries with marginal inputs highly vulnerable. New climate-smart crop cultivars must be developed to address these constraints and ensure food security [47]. As a result, abiotic stressors significantly impact plant growth and yield; high rainfall occurrences may generate floods, while shortage or lack of rainfall over an extended length of time causes drought pressures [48]. There are growing concerns about the quick changes in climatic conditions because adverse weather significantly impacts food security and agricultural productivity. Cropping systems face exacerbated climate impacts with low diversity and high input concentrations and unpredictable crop production owing to environmental changes [49]. More frequent droughts and heavy rains, temperature fluctuations, salinity, and insect pest attacks are imminent, all of which will reduce agricultural yields and raise the risk of starvation [50].

This study emphasized the influence of weather variations on crop wild relatives (CWRs) and its effects on rice genetic resources. Thus, their morphological adaptation to cope with extreme environmental conditions was evaluated for developing climate-smart rice cultivars as the present crop cultivars vary greatly from their wild relatives in terms of phenotypic characteristics. Domestication bottleneck may also increase phenotypic uniformity [51], resulting in consistent phenotypes across environments [52,53]. Agricultural performance may benefit from phenotypic consistency [53]. Plants change their phenotypes in response to their environment. Although formerly thought to be ambient noise, it is now apparent that

(adaptive) phenotypic plasticity involves modifications to exhibit functionally relevant phenotypes under different situations [54]. Consequently, the significance of phenotypic plasticity in crop plant adaptation to environmental variation is yet to be determined.

The current findings identified a location-specific high phenotypic diversity among populations compared to within populations of the CWR of rice, *O. nivara* (Table 3), in line with the previous studies reported [40,55]. Results also revealed that the morphological variation of *O. nivara* was not evenly scattered. The FL-PN-L and FL-A were the most variable traits for *O. nivara* in Sri Lanka. High population-based morphological variations were previously reported in other *Oryza* species in Sri Lanka, but no association was found between those traits and eco-geography [15]. The within-population variation for FL-L showed a relatively higher variation than that of among populations. For example, FL-L variation of the P6 population revealed a higher CV (9.5%) than that of among populations (7.57%) because the phenotypic investigation of this study contained ample sample size to deliver the vital messages on a morphological variation of plant traits. Moreover, *O. nivara* exhibits annual growth habit, early leaf senescence and photoperiod insensitivity, higher inbreeding percentage and continuous flowering [55,56]. Stigmas and anthers are shorter, and panicles are more inserted and close for self-pollination (field observation). Therefore, the within-population diversity is generally lower than that of among populations [57].

Oryza nivara is closely related to domesticated crop species, *O. sativa*. Therefore, it should be given special attention to producing crop varieties that are more tolerant and adaptive to climate change using the prevailing diversity of the natural populations. Furthermore, many species exhibit phenotypic plasticity, indicating that individuals may change their phenotypes in response to their surroundings [58]. When individuals modify their phenotypes across settings in the direction of selection, phenotypic plasticity can be adaptive and enhance fitness across diverse landscapes [59]. Many species are plastic in response to environmental factors. However, scientists do not know whether these plastic modifications benefit under changing climates or are harmful in most situations. Further, adaptive behavioral plasticity in breeding phenology promotes long-term population survival and those populations would be considerably more sensitive to climatic change if plasticity did not exist [60].

4.2 Diversity and Relationships of Morphological Traits

Morphological characteristics have been used as an effective method for determining the genetic diversity of plant genetic resources [61]. Our results showed the morphological variation that existed within and among populations of *O. nivara* in Sri Lanka (Table 3). Some traits measured in this study were significantly different ($P < 0.05$) among populations, and high variance reflected its ability to adapt to a particular habitat resulting in high diversification [16,55]. Plant height is one of the most important traits having the ability to capture more sunlight [62,63]. Results revealed that P5 and P7 populations that grew with other shrubs and weeds had a high variance in plant height. However, the variance for P-H of P5 and P7 populations was not significantly different ($P > 0.05$).

Most of the phenotypic differences of *O. nivara* can be seen in their responses to existing in natural habitats [55]. For instance, vigorous plant growth with the greatest P-H, C-G and AW-L showed in the P3 population from the intermediate zone in Kurunegala district. The higher annual rainfall, suitable soil condition and favourable environment of the intermediate zone (Table 1) in comparison to the dry zone would have resulted in superior development of *O. nivara* in the intermediate zone [64]. Plants in P3 may also resist pest attacks because of their AW-L compared to other populations [65]. The P2 population was slightly morphologically different from the P6 population (Fig. 3), and both P2 and P6 populations were in the coastal line in the dry zone. However, the highest FL-L was recorded in P6, indicating that these plants are adapted to dry environments [66]. Thus, plants have been morphologically adapted for dry, saline conditions and high temperatures to conserve water for survival by reducing P-H, FL-A, and

FL-W, suggesting their adaptation of populations for dry environments [36,55]. However, the P7 population from Siyambalanduwa recorded the highest FL-W and FL-A to intercept more sunlight in competition with weeds and other shrubs [67]. However, the heterogeneous light environment inside a plant canopy results in a range of stress effects for leaves. The adaptation of leaf features to the light gradient [68] from the top to the bottom of the canopy, mostly during leaf creation [69], is one expression of plant phenotypic plasticity. The specific leaf area (SLA, ratio between leaf area and leaf dry mass) is one of the most important morphological features that varies in response to light differences. The SLA plasticity implies morphogenetic regulation of leaves, which prefers to expand leaf area in the shade to intercept more light, although there is a genetic or physiological limitation to total leaf volume as well as a resource limitation [70]. The P7 population was collected from a forest area, scattered as patches, and showed a mixed-growing with other shrubs and weeds (Table 1). However, they were subjected to stress conditions due to competition from other plants. Therefore, plants tend to adjust phenotypically to tolerate the stress conditions [71]. The P1 population in Maradankadawala had the highest value for FL-PN-L as an adaptation to frequent flooding in this habitat [72]. Similar geographically adaptive characteristics have been reported recently [55]. However, the morphological traits measured in this study follow the same ranges reported in IRRI records in species identification. *Oryza nivara* is possibly more appropriate for seasonally dry habitats [55] because of the high mean annual temperature and low precipitation in those regions.

Furthermore, studies on gene expression are essential as it is determined by environmental and genetic factors and varies extremely among populations or species, individuals and within individuals [73]. The influence of local ecological conditions on the genotypic composition of landraces, as well as the close relationship between agroecological factors and plant morphological variation, has previously been explained [74]. Additionally, plasticity may be adaptive in parts of the range subject to temporal fluctuation in environmental circumstances. Moreover, maladaptive or absent in parts of the range subject to less changeable conditions [75]. Few studies have looked into how much plasticity varies intra specifically across the environments [76].

4.3 Implications for the Origin and Adaptation of O. nivara

The higher level of genetic differentiation among populations in *O. nivara* over *O. rufipogon* across different geographies has been well documented [34,36,77]. Similar patterns of morphological variation observed in this study could be attributed to population adaptation to specific environments, exacerbated by habitat fragmentation [33]. Commonly, *O. nivara* in Sri Lanka was found on the edge of ponds, tanks, and beside streams and grown in shallow waters [39,42]. Furthermore, *O. nivara* is found in disturbed habitats, whereas *O. rufipogon* occupies comparatively stable habitats around the globe [78]. Reports highlighted the same phenomenon of ecological adaptation that *O. nivara* habitats have significantly reduced in their scale and size due to agriculture and urbanization [79]. Inbreeding is expected in isolated and small populations, contributing to increasing the genetic differentiation among populations. Further, the presence of a high level of population differentiation in *O. nivara*, explained in terms of different degrees of BPH resistances among populations, has been reported previously [80].

Many studies have suggested modifications in the life history of *O. nivara* populations associated with their habitats [41]. Much evidence has shown that *O. nivara* shifted from persistently wet areas where it originated to seasonally dry areas to adapt to a new environment [33,34,36,81]. In order to adapt to the dry and stressful conditions encountered during this process, phenotypic changes such as shorter life cycles and sexual reproduction may be encouraged. Our results indicated that vigorous plants are found in the P3 population from the intermediate zone (Fig. 1, Table 2). However, *O. nivara* plants from the dry zone also showed adaptive morphological changes for dry and stressful conditions (Table 1), consistent with previous studies [11,33] that found differentiation of morphology, life cycle, and reproductive system to facilitate plant adaptation to diverse habitats conditions.

Lu et al. [82] reported that *O. nivara* is mostly confined to dry habitats with a pronounced dry season but has not been recorded in more moist, western parts of Myanmar. Our study reported that the morphological characters are significantly different among *O. nivara* populations in specific parameters (Table 2), reflecting the ability of ecological adaptation of this wild species because shorter plant height, small culm girth, and erect culm are related to adaptation of *O. nivara* to dry habitats (Fig. 2). Results of our study also supported the assumption of migration of *O. nivara* from wet regions to dry habitats in the country [34]. Some of the morphological differences among seven *O. nivara* populations can be seen as responses to the differences in their genome characters, life cycle, habitat and breeding system [72]. Climate change has the potential to have a significant impact on some natural populations and enhance the risk of extinction for several native species [83]. As a result, researchers propose that future research should use cross-disciplinary integration to examine climate adaptation in a broader range of species. More research is urgently required to produce climate-adaptive crops [84]. The CWRs have a high genetic diversity and can contribute to new genetic diversity for agricultural sustainability [85]. For instance, previous research has indicated that several recently discovered wild rice species in northern Australia have unique alleles for distinct critical traits, which could improve the ability of cultivated rice to withstand climate change [86]. The ability of the same species to display distinct features under different environmental situations is referred to as phenotypic plasticity. A plastic developmental program enables species to detect environmental signals early and produce phenotypes that are more suited to later-life situations. This is frequently used as an adaptive approach for surviving in diverse environments, as long as the plastic reaction is sufficiently rapid, precise, and not too expensive. Despite the direct costs of sustaining plasticity and developing phenotypes, the predictability of the future environment based on environmental signals obtained throughout development is a primary restriction on the utility of phenotypic plasticity of crop wild relatives.

Habitat-specific populations are grouped (Table 1). Both P2 and P5 populations are from similar natural habitats with approximately similar ecological conditions (mean annual temperature and rainfall) (Table 1) of the dry zone and located relatively closer in proximity than other populations (Fig. 1). Sandamal et al. [34] reported a similar clustering pattern according to their genetic basis. Furthermore, P1 and P4 populations were genetically close populations, and they were closely clustered on the basis of the expression of their phenotype. However, genetically very close populations [34], namely P6 and P7, clustered separately based on their morphological differences. The P7 population separated from all populations having the lowest C-G, FL-L and the highest FL-A and FL-W because of its adaptation to shade environment. Additionally, the P1 and P7 populations were also differentiated from the rest (Fig. 3).

Populations from different natural habitats did not cluster together. Morphological adaptation based on habitat specificity is critical for the preserving and long-term usage of the primary gene pool. For *O. nivara* conservation, our results suggest that four out of seven populations should be monitored closely, whereas P1, P3, and P7, as well as one population from P2, P4, P5, and P6, may be utilized for conservation. Contrary to these findings, a population genetic structure study has reported considerable genetic diversity in a particular population [34]. Therefore, further investigations on their morphology, genetic and genomics levels are required to identify populations necessary to give immediate conservation priorities. In addition, *O. nivara* has undergone and still undergoing ecological speciation [55]. In Sri Lanka, most of the *O. nivara* populations can be seen in disturbed habitats [78]. Even in closely related populations, changing environmental circumstances might have affected this CWR adapting to various geographical areas in Sri Lanka. However, natural populations may be able to adapt to changing conditions due to existing plasticity [87], but this plasticity may be insufficient when individuals face future climates that are outside the range of existing environmental variation [88].

5 Conclusion

The genetic diversity of *O. nivara* in Sri Lanka was assessed using their natural populations. A high degree of variability was detected in most of the quantitative traits recorded. The most variable traits were the FL-PN-L and FL-A, whereas the least variable trait was the FL-L. The P7 population, which was collected from a forest area, was adapting to percept more sunlight by increasing FL-W and FL-A while growing with weeds and other shrubs, while P2 and P5 were the most closely related populations among those evaluated. Both P2 and P5 populations were from the same natural habitat in the dry zone with similar ecological conditions in the dry zone. The P3 population from the intermediate zone showed vigorous plant growth with the highest P-H, C-G and AW-L. Genotypic diversity depends on the specificity of the natural habitats and occurs due to morphological variations. The knowledge gained on the diversity of the country specific rice germplasm enhances the conservation efforts of valuable genetic resources, which can be utilized in developing climate-smart cultivars.

Conflicts of Interest: The authors declare that they have no conflicts of interest to report regarding the present study.

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