

RESEARCH ARTICLE

EXPLORING CLIMATE CHANGE IMPACTS ON MORPHOLOGY AND PHENOLOGY OF COMMON WILD RICE IN SRI LANKA

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ABSTRACT

Exploring phenotypic plasticity and adaptive potential of natural populations of wild rice is crucial because of the recent drastic climatic changes. The wild progenitors of cultivated rice (*O. rufipogon* and *O. nivara*) provide an excellent natural system for investigating the processes of phenotypic plasticity. We examine the responses of morphology and phenology of *O. rufipogon* and *O. nivara* in their respective typical natural habitats throughout the life cycle in two distinct periods, 2016 and 2020. A three-year gap was maintained to visualize the variations of traits against the continued climatic effects. Trait divergence between two years was tested using a *t*-test. Results revealed noticeable differences in the morphological characteristics, including the highest plant height (159.92 ± 3.52 cm), flag leaf length (21.15 ± 1.49 cm), flag leaf width (1.16 ± 0.06 cm), anther length (3.84 ± 0.06 mm), and awn length (4.10 ± 0.40 cm) of *O. nivara* in 2020 due to high annual precipitation. *O. rufipogon* showed a stable response, which inhabitant to deep water. Compared to 2016, *O. nivara* flowered earlier in 2020, but *O. rufipogon* displayed a late flowering in 2020. These findings imply that phenotypic plasticity played a significant role in environmental adaptability. These adaptive variations are crucial to adapt in climate change and species divergence, offering new avenues for understanding vital genes for breeding climate resilient rice.

Keywords: climate change adaptation, flowering time, natural habitat, phenotypic plasticity and wild rice

INTRODUCTION

One major concern of the current biodiversity problem is the expected decrease in ecosystem resilience to further changes (climate change, habitat loss and fragmentation) (Oliver *et al.* 2015; Dainese *et al.* 2019). Currently, changes in land use and shifting climatic conditions are recognized as the primary factors leading to worldwide biodiversity decline and the restructuring of biological ecosystems, in several species at different spatial and temporal scales (Parmesan and Yohe 2003; Baillie *et al.* 2004; Vellend *et al.* 2013; IPBES 2019; Daskalova *et al.* 2020). Since the early 20th century, agriculture and forestry have increased significantly across the globe, leading to decreased biodiversity and a

homogeneity of population or species groups (Smith *et al.* 2014). Ecological divergence among populations is frequently attributed to local adaptation driven by divergent natural selection in contrasting environments. Recent observations have highlighted the drastic impacts of climate change in Sri Lanka, with significant alterations in rainfall patterns, temperature fluctuations, and the acceleration of anthropogenic activities such as agriculture, urbanization, deforestation, irrigation canal clearing, road and housing development, and filling of lowlands (Sandamal *et al.* 2021).

These changes in weather patterns have become more pronounced in recent years and have significantly impacted agricultural

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practices, shifting the traditional Yala and Maha seasons upon which the country heavily relies. Alterations in rainfall patterns emerge as one of the prominent drivers of ecological divergence, potentially affecting the survival and distribution of wild rice species (Liyanage and Senanayake 2010; Sandamal *et al.* 2018a).

Common wild rice, *O. rufipogon* and *O. nivara*, the wild progenitors of domesticated Asian cultivated rice (*O. sativa*), exhibit considerable ecological and phenotypic divergence, adapting to a vast range of habitats in Sri Lanka with diverse ecosystems (Sandamal *et al.* 2021; 2022; Jing *et al.* 2023; Kovach *et al.* 2007; Sang and Ge 2007). *O. rufipogon* is a perennial plant that primarily undergoes cross-fertilization and is sensitive to photoperiods, typically found in consistently moist environments. Conversely, *O. nivara* is an annual plant that is predominantly self-fertilizing, not sensitive to photoperiods, and is found in habitats that are either seasonally dry or experience seasonal flooding (Kovach *et al.* 2007; Liu *et al.* 2015; Sang and Ge 2007; Vaughan *et al.* 2008; Zheng and Ge 2010). *O. rufipogon*, found in deep-water swamps, is characterized by its tall stature, mixed mating system, photoperiod sensitivity resulting in late flowering, and abundant vegetative reproduction. Conversely, the annual species *O. nivara*, noted for its short stature, resulting in early flowering, is adapted to seasonally dry environments and prioritizes a greater allocation of resources towards sexual reproduction (Grillo *et al.* 2009; Banaticla-Hilario *et al.* 2013).

The significance of this diversity was suggested several years ago and has been successfully proven by multiple studies utilising a range of model organisms (Lowry *et al.* 2008; Nakazato *et al.* 2008; Banaticla-Hilario *et al.* 2013). Phenology and morphological variation have significant theoretical implications for understanding evolutionary processes, climate change adaptation and population divergence (Rundle and Nosil 2005). Plant phenology and morphology variations can influence various ecological interactions and climate change. However, most of the previous studies have

concentrated on *ex-situ* or common garden experiments and neglected to capture the natural environmental interactions and adaptive responses in natural settings. For instance, studying the timing of flowering can provide insights into the environment and ecological niche of a species and its role in the natural ecosystem and potential adaptive significance of these traits (Thompson 2005; Schluter 2022). Despite significant efforts, many crucial questions about the phenology and morphological diversity of natural populations remain unresolved in Sri Lanka due to difficulties in continued observation. One of the most contentious issues is the divergence of phenological and morphological novelty, adaptive divergence of natural populations and ongoing climate change. Thus, this study is critical for the scientific community as it addresses the gap in understanding the real-time adaptive responses of wild rice natural populations to rapid environmental and climatic changes.

The objectives of this research are to compare morphological traits within and between *O. rufipogon* and *O. nivara* in their typical natural habitats over two distinct periods, 2016 and 2020, to elucidate the influence of environmental variables on phenological traits and to determine the phenotypic plastic responses of these species to their natural habitats.

MATERIALS AND METHODS

Study Populations

To investigate major phenological and morphological differences that might shape to natural environment, we selected two typical natural populations of *O. rufipogon* and *O. nivara* in Thihagoda [(06°00'01" N; 80°33'43" E), (Wet Zone)] and Maradankadawala [(08°07'44" N; 80°33'46" E), (Dry Zone)], respectively (Figure 1).

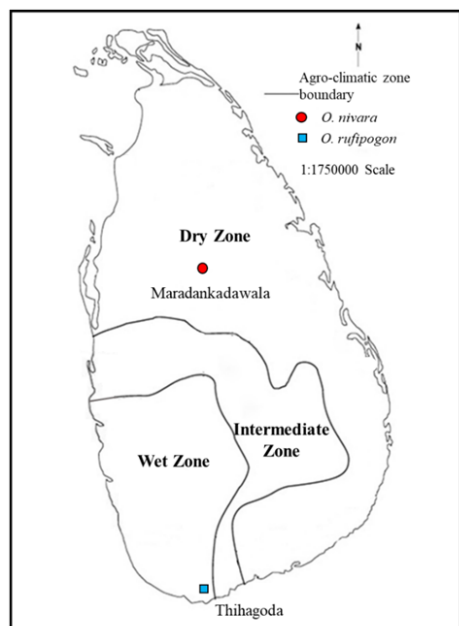


Figure 1: Sampling locations (*in-situ* natural population). Solid lines represent the divisions of the wet zone, dry zone and intermediate zone in Sri Lanka

The study was conducted throughout the year for two distinct periods, 2016 and 2020. Our previous study indicated that two sites have relatively minor human interference and represent the typical communities of native plants (Sandamal *et al.* 2022). The date of first flowering (flowering stage) and seed setting (mature stage) were recorded (Table 1) under the phenological observations. Flowering time is critical for plants to synchronize their reproductive cycle with optimal environmental conditions, and the process of seed set is crucial for viable (mature) seed production (Mazer *et al.* 2022; Vicentini *et al.* 2023). This synchronization

ensures that plants maximize their reproductive success under different climatic conditions. Further, we examined six morphological traits (Table 1) that were considered to be either taxonomically important or adaptive.

Natural Habitats

We selected two typical natural habitats with minimal human interference to ensure representative applicability. Populations of *O. rufipogon* are inhabitant to deep water irrigation canals or deep marshy lands at consistent water availability and confined to wet zone. This particular population was located in a deep-water irrigation canal; dimensions ranging from 3 to 5 m wide and 1 to 3 m deep. This population is dense and represented the typical growth patterns of the species (Figure 2A). However, this population is increasingly endangered by periodic cleaning of irrigation canal and agriculture. In contrast, *O. nivara* is confined to dry zone and the selected typical population was spread near a lake area and mixed grows with other grasses and weeds. Seeds germinate at the beginning of the rainy season and plants flower and produce seeds before the next dry season. There were several populations of plants in the area; some were located next to a road and separated by fields, some were found on both sides of the main road and one of the populations was situated in a marshy area (Figure 2B). The area was frequently subjected to flooding (0.5 m water level) in the rainy season and almost completely dry in the dry season and generally prefers shallow water, habitats with water levels reaching up to 1 meter during the rainy season. These two

Table 1: Morphological traits and their method of measurement

Trait (Abbreviation)	Method of trait measurement
Morphology	
Plant height (PH)	Height from base to the tip of the plant.
Flag leaf length (FLL)	Length of the flag leaf, from the ligule to the tip of the blade and record the average length of three leaves.
Flag leaf width (FLW)	The widest width of the flag leaf. Record of the average of three leaves.
Flag leaf angle (FLA)	The angle from the panicle axis to the flag leaf. Record of the average of three panicles.
Anther length (ANL)	Length of anther when the spikelet about to bloom. Record of the average of three anthers.
Awn length (AWL)	Length of awn on top of panicle after anthesis. Record of the average of three awns.
Phenology	
Flowering stage	Number of tillers in the natural population at the flowering stage.
Mature stage	Number of tillers in the natural population at the mature stage.

populations are representative of typical habitats suitable for investigating two species' responses to changing environmental patterns, making them excellent platforms for such research. Rainfall data were collected from the nearest weather stations of the respective locations in Sri Lanka; Farm Mechanization Research Centre (FMRC), Mahailuppallama (08°10'73" N; 80°46'46" E), and the Faculty of Agriculture, University of Ruhuna (06° 06'13" N; 80°56'84" E).

These populations displayed typical growth habits in natural settings of wet and dry zones (Figure 2).



Figure 2: Natural habitat of *O. rufipogon* (A) and *O. nivara* (B) populations

We placed three 1 m² plots for each population, positioning them at 3 m intervals around the location with the highest plant density. Observations were collected in three distinct plots as replicates at two-weeks interval during entire growth season from

March 2016 to June 2017 and from June 2020 to July 2021. The observation period was aligned to the seedling emergence which is comparable to the rainy season (In 2016, the rainy season started earlier than in 2020).

Data Analysis

In the present study, we examined the variations in morphological and phenological traits over two separate years, 2016 and 2020, within the natural populations of *O. rufipogon* and *O. nivara*. The study indicated the measurement of six morphological and two phenological traits in their respective natural habitats. All morphological analyses were conducted using Minitab 17. Microsoft Excel was also used to compare the divergence of phenological traits between different two-year periods in *in-situ* habitats. The *t*-test was conducted to test trait divergence between two years. Boxplot analysis was performed to determine the morphological divergence of both species over different years.

RESULTS AND DISCUSSION

Morphological Variation

Our overall results revealed that, particularly in 2020, *O. nivara* population exhibited significantly higher growth values such as plant height (PH; 159.92 ± 3.52 cm), flag leaf length (FLL; 21.15 ± 1.49 cm), flag leaf width (FLW; 1.16 ± 0.06 cm), anther length (ANL; 3.84 ± 0.06 mm), and awn length (AWL; 4.10 ± 0.40 cm), with the exception of flag leaf angle (FLA; 71.22 ± 7.23) indicating a pronounced display of phenotypic plasticity. In contrast, the *O. rufipogon* population did not show significant differences between the years 2016 and 2020, suggesting a degree of phenotypic stability across temporal scales (Table 2).

Table 2: Evaluation of morphological traits of *O. rufipogon* and *O. nivara* in natural populations between 2016 and 2020

Trait	<i>O. nivara</i>		<i>P</i> value	<i>O. rufipogon</i>		<i>P</i> value
	Mean ± SE			Mean ± SE		
	2016	2020		2016	2020	
PH (cm)	150.93 ± 3.14	159.92 ± 3.52	0.000	92.13 ± 2.13	111.27 ± 1.55	0.065
FLL (cm)	19.07 ± 1.05	21.15 ± 1.49	0.000	20.42 ± 0.51	27.85 ± 1.10	0.262
FLW (cm)	01.02 ± 0.04	01.16 ± 0.06	0.000	00.90 ± 0.01	01.25 ± 0.02	0.108
FLA (°)	76.80 ± 4.67	71.22 ± 7.23	0.117	79.40 ± 1.42	87.76 ± 4.70	0.523
ANL (mm)	03.80 ± 0.02	03.84 ± 0.06	0.006	02.98 ± 0.08	03.26 ± 0.04	0.622
AWL (cm)	04.23 ± 0.24	04.10 ± 0.40	0.000	06.27 ± 0.10	10.75 ± 0.16	0.791

Moreover, boxplot analysis supported the findings from the two-sample *t*-test, presenting clear demarcations between the two observed years for each species, with *O. nivara* showcasing more extensive morphological variation compared to *O. rufipogon* due to the variations of mean annual temperature and low rainfall in dry zone (Figures 3 & 4). This alteration is attributed to the favourable environmental conditions experienced during this period. As precipitation exponentially increased in the dry zone in the year 2020, *O. nivara* demonstrated superior performance, underlining its adaptability and the critical role of environmental factors in shaping phenotypic plasticity. This emphasizes the species' inherent capacity for phenotypic plasticity, enabling it to survive and thrive in the face of changing climatic conditions. However, *O. rufipogon* exhibited a more consistent phenotypic expression over time from 2016 to 2020. This distinction may illuminate the adaptive responses elicited by varying natural conditions experienced across

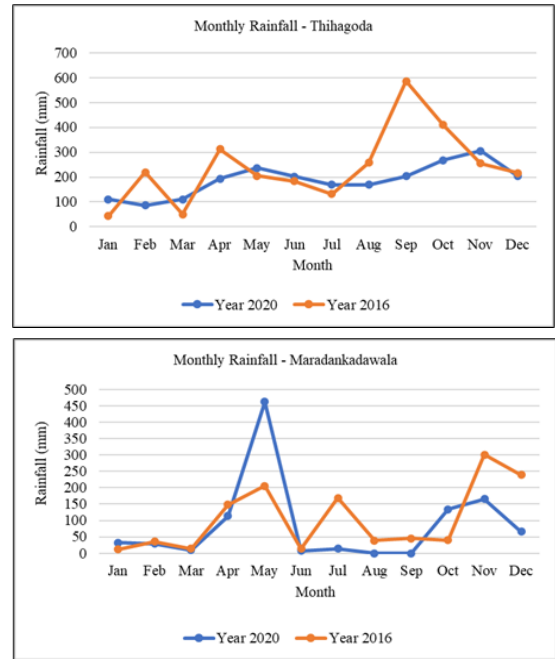


Figure 4: Monthly rainfall distribution of Maradankadawala and Thihagoda during the experimental period (2016 and 2020)

the years studied. It highlights the inherent capacity for plasticity among morphological

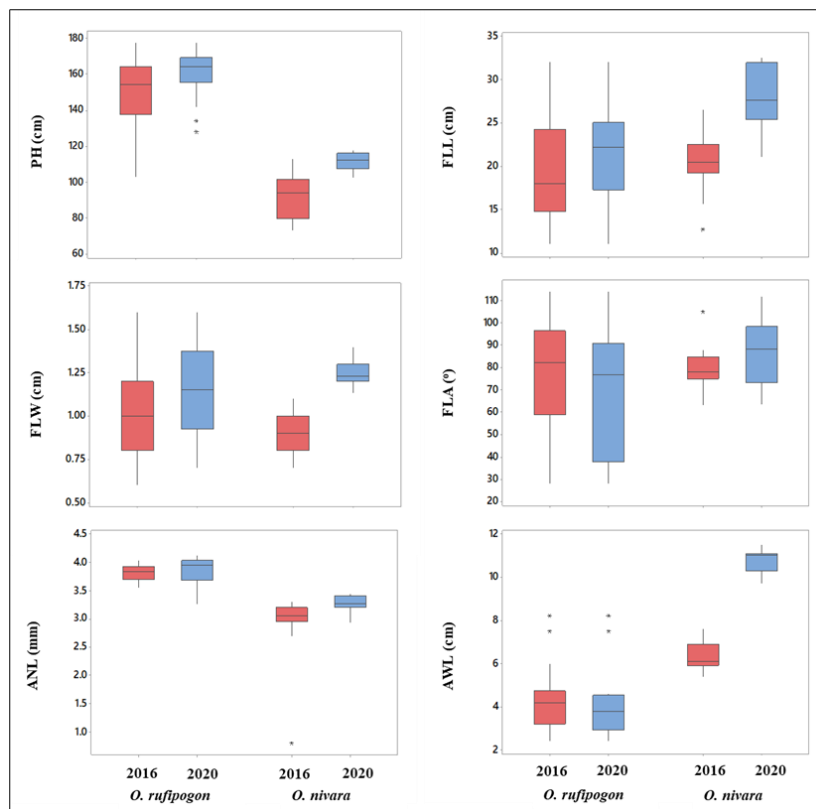


Figure 3: Morphological traits of *O. rufipogon* and *O. nivara* in both populations across two different years (2016 and 2020).

Outliers are marked by stars (*)

traits in wild rice species, possibly facilitating their survival and adaptation in fluctuating environmental conditions.

We observed noticeable differences in the morphological traits of *O. nivara* than *O. rufipogon* in two different years. These variations provide crucial information on morphological trait modification's role in species adaptation and differentiation. This divergence possibly reflects the higher phenotypic plasticity shown by *O. nivara*, an important adaptive response to environmental variations and might potentially enhance survival in different environmental conditions. This adaptation is critical to the survival of the species, particularly in settings where environmental factors like temperature and moisture availability are prone to large temporal fluctuations. Moreover, the presence of phenotypic plasticity in *O. nivara* supports the theoretical prediction that populations living in diverse habitats are more likely to exhibit a broader range of adaptive responses (Ghalambor *et al.* 2007; Sultan 2000). Most of the phenotypic variations in *O. nivara* are evident in their adaptations to natural habitat (Banaticla-Hilario *et al.* 2013; Sandamal *et al.* 2022). While advantageous in fluctuating environments, such plastic responses may also entail costs or trade-offs that could influence evolutionary trajectories and speciation processes (Agrawal 2001; DeWitt *et al.* 1998). Historically, climate change occurred over long periods of time. However, a significant increase in the magnitude of climate alterations has been noticed in recent years (Rosenzweig and Neofotis 2013). These climatic transformations have previously happened at a slower rate, and thus, effects imposed on ecosystems were insignificant. However, the current rapid pace of climate change presents a significant threat to the survival and ecological stability of natural populations. *O. nivara* has shown impressive adaptability despite rapid environmental changes, exhibiting phenotypic modifications that enhance its capacity to survive in different climatic conditions (Grillo *et al.* 2009; Sandamal *et al.* 2022; Wijerathna *et al.* 2022). In contrast, *O. rufipogon* is less

influenced by these changes, most likely because it generally inhabits moist environments that have been somewhat adapted to wet environment conditions (Huang and Schaal 2012; Liu *et al.* 2015). The difference in reaction emphasises the diverse levels of resilience and adaptation across species when challenged with the current rate of climate change.

In order to protect these species and minimise the threat of extinction, it is crucial to understand and support their adaptation processes in response to environmental changes. Given the ongoing adaptation of *O. nivara* to changing environments, it is vital to prioritise conservation initiatives to the preservation of genetic diversity and the integrity of habitats. This is especially important for species like *O. rufipogon*, as their apparent stability may conceal hidden vulnerabilities.

Phenotypic divergence is the first step towards local adaptation and speciation and has thus been extensively explored across plant species (Mazer *et al.* 2022; Mitchell-Olds *et al.* 2007; Richardson *et al.* 2014; Rieseberg *et al.* 2002; Wadgyamar *et al.* 2022). Previous results indicate a substantial link between the variation of morphological traits and several major climatic/environmental factors, including altitude, temperature, and rainfall (Banaticla-Hilario *et al.*, 2013; Liu *et al.*, 2015). However, according to our knowledge, no information is available describing the phenotypes of *in-situ* habitats in Sri Lanka for different years. In response to climatic factors, we observed both species have evolved distinct phenotypes to adapt to changing climate condition and expanded in range. For instance, predominantly vegetative propagation, longer and more spreading culms make *O. rufipogon* better adapt to permanently inundated habitats; whereas being annual, shorter and less decumbent culms of *O. nivara* are more suitable for seasonally dry habitats (Banaticla-Hilario *et al.* 2013; Sandamal *et al.* 2018b; Cai *et al.* 2019; Sandamal *et al.* 2021). Congruent with ecological speciation (Cai *et al.* 2019; Meng *et al.* 2024; Sandamal *et al.* 2018a; Zheng and

Ge 2010), the differences in morphological traits between *O. rufipogon* and *O. nivara* are mainly explained by the distinct habitats they grow and have important implications for their ecological adaptation and evolutionary dynamics.

Moreover, scientists hypothesize that the annual species *O. nivara* may have originated from the perennial *O. rufipogon* due to a habitat shift from wet to dry environment. Consequently, *O. nivara* is commonly found in dry areas, while *O. rufipogon* occupies more consistent, wet habitats. *O. rufipogon* consistently prefers for its habitat, while *O. nivara* shows adaptable and plastic responses to changes in the environment. These findings highlight the important evolutionary mechanisms that allow species like *O. nivara* to adapt to rapid environmental changes. This emphasises the necessity for continued research to gain a deeper understanding of these adaptive processes and their

implications for conservation and biodiversity management in the face of increasing climate change challenges.

Phenological variation

Our *in-situ* observation of the life cycle of *O. rufipogon* and *O. nivara* populations for an entire year of 2016 and 2020 showed substantial differences in flowering phenology between two years of each species, including both flowering stage and mature stage (Figure 5). The differences occurred across both the flowering and maturity stages of the species' life cycles. Our analysis reveals that *O. rufipogon* population exhibit a more extended life cycle, ranging from 7 to 12 months, in stark contrast to the shorter 4 to 5-month life cycle of *O. nivara* species as depicted in Figure 5. Particularly, *O. rufipogon* exhibited the flowering pattern with two distinct peaks, whereas *O. nivara* population showed a single peak of flowering.

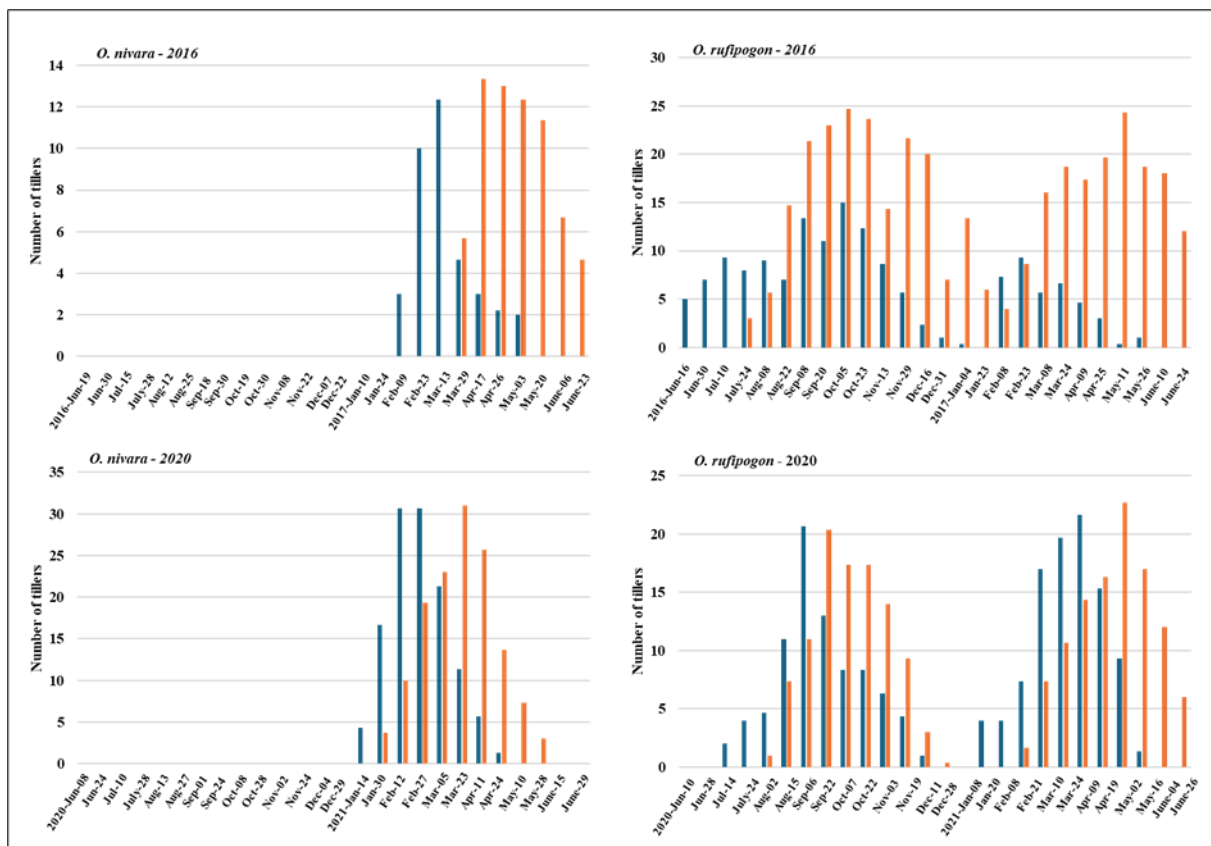


Figure 5: Phenological traits (flowering stage and mature stage) of *O. nivara* and *O. rufipogon* in natural population in two distinct year 2016 and 2020. The flowering and mature stages are indicated by blue and yellow colours, respectively

In 2020, *O. nivara* exhibited earlier flowering compared to 2016, whereas *O. rufipogon* displayed the opposite pattern in both years. Similar trends were noted for both species with minor variations. In the native population of *O. nivara*, seeds germinated at the beginning of the rainy season, and the plants flowered and produced seeds prior to the start of the dry season (Sang and Ge 2007). The *O. nivara* population displayed almost identical patterns, whereas the *O. rufipogon* population exhibited slight variations in their life cycle between the two years. The discrepancy is probably attributed to the distinct climates in the two years; the *O. rufipogon* population inhabits in wet environments with continuous water availability, whereas the *O. nivara* population is distributed in marshy areas subject to periodic flooding.

Flowering phenology plays a pivotal role in the mechanisms of ecological adaptation and the speciation process, drawing significant attention in plant research (Franks 2015; Mazer *et al.* 2022; Nakazato *et al.* 2008; Osborne *et al.* 2019; Wunder *et al.* 2023). Flowering time contributes to genetic differentiation and triggers the divergence of traits as species adapt to their environmental niches (Lowry *et al.* 2008; Servedio *et al.* 2011; Sugai *et al.* 2023). Although there has been considerable attention given to flowering time in cultivated rice varieties (Oka 1988; Vicentini *et al.* 2023), the investigation of flowering phenology and its diversity within and among wild rice species such as *O. rufipogon* and *O. nivara* has been relatively limited, despite some research attempts (Morishima *et al.* 1984; Oka 1988; Xu *et al.* 2020; Sandamal *et al.* 2021; Wijerathna *et al.* 2021). Nevertheless, among the several methods used, *in-situ* observation has received less focus because of the challenges involved in manipulating and observing wild populations, especially those of non-model species (Anderson *et al.* 2012; Mazer *et al.* 2022; Park and Post 2022; Sugai *et al.* 2023). Present study uncovers differences in the timing of biological events in natural settings, both within and across species, throughout different periods. This demonstrates the

complex relationship between genetic factors and environmental conditions in shaping these biological traits.

The present investigation revealed varying degrees of phenological variation between species across different years by *in-situ* observation of their natural habitat. The variation observed can be attributed to genetic factors and climate variables, specifically precipitation and temperature (Morishima *et al.* 1984; Kuroda *et al.* 2005; Sang and Ge 2007; Vaughan *et al.* 2008; Cai *et al.* 2019). Moreover, we discovered drastic differences between species in the flowering phenology, as demonstrated by *in-situ* observation. Sandamal *et al.* (2021) found that *O. rufipogon* exhibited a long-life cycle characterised by two distinct phases of flowering, whereas *O. nivara* had a considerably shorter life cycle with only one phase of flowering pattern. This illustrates differences in the typical conditions or habitats where *O. rufipogon* (found in the wet zone) and *O. nivara* (found in the dry zone) grow. The occurrence of bimodal and single-modal reproductive phases may be attributed to distinct adaptation strategies developed in response to ecological or climatic challenges. Based on the present study, *O. rufipogon* exhibited a delayed flowering pattern in 2020 compared to 2016. In addition, the flowering period for *O. rufipogon* during its first peak was considerably longer in 2016 (7 months) than in 2020 (5 months). However, the drastic climatic fluctuations led to a decrease in both the flowering period and the peak of flowering periods in the year 2020. Another crucial aspect is that in 2016, there were two distinct peaks in a continuous life cycle, whereas in 2020, there were also two peaks, but with a deceleration in the middle (between two peaks). Evidently, the data demonstrates that climate variables fluctuate for the identical population over several years. Due to its sensitivity to photoperiod, the *O. rufipogon* population in Southern China exhibited a single peak in response to the local climate (Zhou *et al.* 2013). Understanding climate fluctuations mostly relies on the identification of drastic variation in flowering peaks and phases. However, *O. nivara* exhibited

contrasting flowering phenology in two distinct years. The evidence indicates that the flowering period or life cycle of *O. nivara* is highly flexible (plastic response) and sensitive to variations in climate changes. Of 2020, there was early flowering, mainly due to changes in rainfall patterns (Figure 4). The temperature distribution pattern of both tested years did not show significant differences in both respective locations (Data not shown). This finding is confirmed by studies conducted by Liu *et al.* (2015), Sandamal *et al.* (2021), Sang and Ge (2007), and Vaughan *et al.* (2008). Moreover, the flowering period remained similar between 2016 and 2020.

However, there was an apparent shift in the flowering time, as shown in Figure 4. The flowering phenology of both species can vary to some extent in response to fluctuating climate conditions. This encourages previous statements that adaptability is crucial for species to adapt to different ecological conditions and might influence their speciation processes (Anderson *et al.* 2012; Fox *et al.* 2019; Levin 2009).

CONCLUSIONS

The findings of this study indicate that phenotypic plasticity and adaptive potential of *O. nivara* and the phenotypic stability of *O. rufipogon* under varying climatic conditions in Sri Lanka. The observed morphological and phenological variations between two species over different years highlight the critical role of environmental factors, mainly precipitation and temperature in shaping these traits. While *O. nivara* demonstrated remarkable plasticity, adapting to rainfall fluctuation patterns and thriving in seasonally dry habitats, *O. rufipogon* exhibited stability, reflecting its preference for consistent moist environments. Results emphasize the evolutionary strategies that enable these wild rice species to cope with climatic changes, offering valuable insights for breeding climate-resilient rice varieties. Future studies are necessary to elucidate the underlying genetic mechanisms driving these adaptive traits and contributing to the plant adaptation

and speciation under global climate change pressures.

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AUTHOR CONTRIBUTION

DR designed and supervised the study. PW and SS performed the experiment, analysed the data and wrote the original draft. DR critically revised the manuscript.

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