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*SHORT COMMUNICATION*

# VARIABILITY IN DROUGHT SENSITIVITY OF UPLAND RICE VARIETIES USED IN MADAGASCAR'S CENTRAL HIGHLANDS

## VARIABILITÉ DE LA SENSIBILITÉ À LA SÉCHERESSE DES VARIÉTÉS DE RIZ PLUVIAL UTILISÉES SUR HAUTES TERRES CENTRALES DE MADAGASCAR

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## ABSTRACT

In Madagascar's Central Highlands, 70% of farmers depend on upland rice (*Oryza sativa* L.) for their livelihoods. However, these agrosystems are increasingly exposed to drought due to erratic climate change effects and decreasing rainfall. The objective of this study was to explore the variability in drought sensitivity of local upland rice varieties, which are characterised by low genetic diversity due to strong selection for cold tolerance and blast resistance. A greenhouse experiment was conducted, where five upland rice varieties commonly used by farmers, namely Chhomrong Dhan (the control variety), FOFIFA 173, FOFIFA 186, FOFIFA 200 and FOFIFA 201, were subjected to four soil water regimes, representing increasing levels of drought stress. These treatments included well-watered (control), rolling stage, drying stage and death stage. Results showed that under each soil water regime, none of the tested varieties differed significantly from the control variety, Chhomrong Dhan, in terms of biomass production. However, FOFIFA 186 and FOFIFA 201 exhibited a 2–3 days delay in the onset of drought stress symptoms, and survived longer. Such a delay represents a meaningful advantage in Madagascar's Central Highlands, where consecutive dry days are frequent at the beginning of the cropping season. This response may reflect more conservative water-use strategies and/or

greater physiological tolerance to drought. However, further studies are required to confirm the underlying mechanisms. These findings provide valuable insights for future research and breeding programmes aimed at improving the climate resilience of upland rice in Madagascar's Central Highlands.

*Key Words*: Drought stress, genetic diversity, physiological tolerance

## RÉSUMÉ

Sur les Hautes Terres Centrales de Madagascar, 70 % des agriculteurs dépendent du riz pluvial (*Oryza sativa* L.) pour leur subsistance. Cependant, ces agrosystèmes sont de plus en plus exposés à la sécheresse en raison de l'irrégularité et de la diminution des précipitations. L'objectif de cette étude était d'explorer la variabilité de la sensibilité à la sécheresse des variétés locales de riz pluvial, qui sont caractérisées par une faible diversité génétique due à une forte sélection pour la tolérance au froid et la résistance à la pyriculariose. Une expérimentation en serre de six semaines a été menée, au cours de laquelle cinq variétés de riz pluvial couramment utilisées par les agriculteurs, à savoir Chhomrong Dhan (variété témoin), FOFIFA 173, FOFIFA 186, FOFIFA 200 et FOFIFA 201, ont été soumises à quatre régimes hydriques du sol, représentant des niveaux croissants de stress hydrique : bien arrosé (témoin), stade d'enroulement, stade de dessèchement et stade plante morte. Les résultats ont montré que, pour chaque régime hydrique du sol, aucune des variétés testées ne différait significativement de la variété témoin, Chhomrong Dhan, en termes de production de biomasse. Cependant, FOFIFA 186 et FOFIFA 201 ont présenté un retard de 2–3 jours dans l'apparition des symptômes de stress hydrique, et ont survécu plus longtemps. Un tel délai représente un avantage significatif sur les Hautes Terres Centrales de Madagascar, où les jours secs consécutifs sont fréquents au début de la saison de culture. Cette réponse peut refléter des stratégies d'utilisation de l'eau plus conservatrices et/ou une plus grande tolérance physiologique à la sécheresse. Toutefois, des études supplémentaires sont nécessaires pour confirmer ces mécanismes sous-jacents. Ces résultats fournissent donc des informations précieuses pour les futurs programmes de recherche et de sélection visant à améliorer la résilience climatique du riz pluvial sur les Hautes Terres centrales de Madagascar.

*Mots Clés*: Diversité génétique, stress hydrique, tolérance physiologique

## INTRODUCTION

As the staple food for about half of the world's population, rice (*Oryza sativa* L.) plays a vital role in global food security (de Sousa *et al*., 2023). As the world's population grows, there will undoubtedly be a greater demand for rice, thus underscoring its vital role in ensuring global food security. In Africa alone, rice demand quadrupled between 1990 and 2018 (Fiamohe *et al.*, 2018; De Vos *et al*., 2023), yet future projections indicate that it will double again by 2050 (Yuan *et al*., 2024).

To meet this growing demand, rainfed rice is becoming increasingly important, especially in regions where irrigable areas are scarce. Indeed, in some regions, a significant proportion of farmland depends exclusively on rainfall (Biazin *et al*., 2012). Unfortunately, these ecosystems are facing serious challenges, as a result of climate change.

More than one-third of the world's total farmland is seriously affected by drought (Panda *et al.,* 2021), and rainfed agrosystems, which lack access to irrigation, are the first to suffer under such conditions. For rice, which is a water-demanding crop, drought stress drastically reduces plant growth and development, and ultimately reduces grain yield (Panja *et al.*, 2022; Jarin *et al*., 2024a). In extreme cases, rice crops can even fail completely (Panja *et al.*, 2022). Therefore, drought stress is recognised as one of the main limiting factors for rice production in rainfed

ecosystems (Habibpourmehraban *et al.*, 2023). As such, it poses a serious threat to global food security in regions that depend on this crop.

This problem is particularly critical in Madagascar, especially in the Central Highlands, where the extension of new irrigated lowland rice is almost impossible (Raboin *et al.*, 2010; 2013). More than 70% of farmers in these regions cultivate rainfed upland rice and depend on it for their livelihoods (Ramanitrinizaka *et al.*, 2023). However, the climate trends in these regions indicate erratic rainfall patterns and an increased frequency of drought periods, with frequent delays in the onset of the first rains (Leroux *et al.*, 2023), which can lead to significant yield losses.

Given this situation, there is an urgent need to develop effective strategies to strengthen the climate resilience of these agroecosystems. One of the first strategies that should be explored is the implementation of varietal improvements geared towards rice varieties that are better adapted to drought stress. Indeed, breeding for drought-tolerant varieties is the sustainable way of enhancing rice productivity in the current climate change context (Hassan *et al.*, 2023). However, upland rice in Madagascar's Central Highlands is characterised by low genetic diversity. Although upland rice breeding in the region began in the 1990s, the genetic base remains limited, principally due to strong selection pressure for cold tolerance and blast resistance (Raboin *et al*., 2010; 2013; Ramanitrinizaka *et al*., 2023). The objective of this study was to explore variability in drought sensitivity of local upland rice varieties in Madagascar's Central Highlands, in order to provide potential avenues for future research and breeding programmes focusing on drought tolerance.

## MATERIALS AND METHODS

**Experimental design.** In this preliminary study, simple indicators were used to assess the variability in drought sensitivity among varieties. These indicators were based on observations of leaves rolling and drying at the vegetative stage (IRRI, 2014). A six weeks greenhouse experiment was, therefore, conducted in the Laboratory of Radioisotopes at the University of Antananarivo, Madagascar.

Cylindrical PVC pots, 30 cm height and 16 cm diameter, were filled with 5 kg of soil collected at a depth of 0-10 cm, from a natural savannah in the eastern part of the Itasy region (19°05'40''S; 47°25'65''E). The soil corresponds to a typical Ferralsol of the Central Highlands of Madagascar, characterised by high acidity, severe nutrient depletion, and a dominance of fine fractions, as detailed in Table 1.

The soil was air-dried, sieved at 5 mm, and thoroughly homogenised before use. A net was attached to the bottom of the cylinder to support the soil, and filter paper was placed over the net to prevent soil from escaping; while allowing water to drain away. The soil was fertilised with farmyard manure.

To reflect farmers' practices, the manure was applied locally in a planting hole of approximately 8 cm deep, positioned at the centre of each pot. Farm yard manure (24 g) of dry manure was applied in the hole, corresponding to the average amount of manure applied to each planting hole in upland rice cultivation, for a standard dose of 6 t $ha^{-1}$. To ensure uniform seedling emergence, the rice grains were pre-germinated before sowing.

TABLE 1. Main physicochemical characteristics of the soil used in the experiment

| Property | Value |
|---|---|
| Soil type | Ferralsol |
| pH (H, O) | 4.7 |
| pH (KCl) | 4.0 |
| Total N (%) | 0.21 |
| Available P (mg $kg^{-1}$) | 0.47 |
| Exchangeable Ca ($cmol^{+}$ $kg^{-1}$) | 0.42 |
| Exchangeable Mg ($cmol^{+}$ $kg^{-1}$) | 0.15 |
| Exchangeable K ($cmol^{+}$ $kg^{-1}$) | 0.06 |
| Texture (clay + fine silt) | 71% |

The grains were placed on a moistened paper towel and kept at 26°C for a period of three days. Then, three pre-germinated rice grains were sown in the hole and covered with a thin layer of soil.

Five upland rice varieties were selected for this experiment. Three of these varieties; Chhomrong Dhan (CD), FOFIFA 173 (F173) and FOFIFA 186 (F186) have been widely used by farmers in the Central Highlands for several years. The other two, FOFIFA 200 (F200) and FOFIFA 201 (F201) are new varieties that have recently been released, but have already been very well received by farmers. The CD variety was considered as the control variety, given that it is the standard variety most widely used in Madagascar's Central Highlands. All five varieties are blast-resistant and generally demonstrate good tolerance to cold, albeit to different extents. A brief description of these five varieties is given in Table 2.

During the first two weeks of the experiment, all pots were watered three times a week to field capacity of the soil. From the third week, different soil water regimes were established, corresponding to different levels of drought stress. The leaf rolling and drying scales (Table 3) of the Standard Evaluation System for rice (IRRI, 2014) were used to delineate the different levels of drought stress.

Four soil water regimes were established; (i) well-watered (control), where the soil was continuously watered at field capacity throughout the experiment; (ii) rolling stage, where soil watering was temporarily stopped until all plants reached at least the level 5 of the leaves rolling scale (Table 3). Once this level of stress was reached, the soil was re-watered and maintained at field capacity; (iii) drying stage, where soil watering was temporarily stopped until all plants reached at least the level 3 of the leaves drying scale (Table 3). Once this level of stress was reached the soil was re-watered and maintained at field capacity; (iv) death stage, where soil watering was stopped until the plant died definitively, i.e., when the plant had lost all its greenery and the base of the stem became brittle.

TABLE 2. Description of the varieties used in the experiment. The following information was taken from the official technical data sheets of the varieties

| Variety | Geographical origin | Breeding stock | Breeder | Year of release in Madagascar | Potential yield | Tolerance to cold |
|---|---|---|---|---|---|---|
| Chhomrong Dhan (CD) | Nepal | Unknown | Unknow | 1995 | 6.4 t $ha^{-1}$ | Very good |
| FOFIFA 173 (F173) | Madagascar | Chhomrong Dhan x Unknown | FOFIFA & CIRAD | 2012 | 6.5 t $ha^{-1}$ | Medium |
| FOFIFA 186(F186) | Madagascar | Chhomrong Dhan x Sucupira | FOFIFA & CIRAD | 2015 | 7 t $ha^{-1}$ | Good |
| FOFIFA 200(F200) | Madagascar | Chhomrong Dhan x Yunlu 48 | FOFIFA & CIRAD | 2023 | 7.8 t $ha^{-1}$ | Very good |
| FOFIFA 201 (F201) | Madagascar | FOFIFA 172 × Exp 206 | FOFIFA & CIRAD | 2023 | 8 t $ha^{-1}$ | Good |

TABLE 3. Scale of rice leaves rolling and leaves drying in response to drought stress (IRRI, 2014)

| Scale | Leaves rolling | Leaves drying |
|---|---|---|
| 0 | Leaves healthy | No symptoms |
| 1 | Leaves start to fold (shallow) | Slight tip drying |
| 3 | Leaves folding (deep V-shape) | Tip drying extended up to 1/4 |
| 5 | Leaves fully cupped (U-shape) | 1/4 to 1/2 of all leaves dried |
| 7 | Leaf margins touching (O-shape) | More than 2/3 of all leaves fully dried |
| 9 | Leaves tightly rolled (V-shape) | All plants apparently dead. Length in most leaves fully dried |

It should be noted that at the rolling and drying stage treatments, the soil was not re-watered until all plants of each variety reached the targeted stress level. Therefore, it is possible that some plants exceeded the targeted stress level before being re-watered. This approach ensured that all plants were subjected to the same duration of drought, although the intensity of stress may have varied among individuals.

Each treatment was replicated four times, resulting in a total of 80 pots (5 varieties x 4 water regimes x 4 replicates). The pots were randomly arranged on a table in the greenhouse, in a completely randomised design. The pot positions were rotated daily to ensure uniform experimental conditions. The mean day and night temperatures in the greenhouse were 29.11 ± 6.02 °C and 15.30 ± 2.29 °C (mean ± standard deviation), respectively.

**Plant measurements.** During the drought period, the leaves of the rice plants were inspected daily at a fixed time (8 a.m.) for evolution of signs of rolling and drying (Table 3). The duration of drought required to reach each stress level was carefully recorded. At the end of the experiment, the pots were dismantled, and the dry weights of the total shoot and root biomass of the rice plants were measured.

**Soil measurements.** Soil water content was measured throughout the experiment, by weighing the pots three times a week, at 2 days intervals. Also, soil water potential was monitored, using a setup of six Teros 21 sensors, connected to a ZL6 data logger (Meter Group, Germany). Soil water potential reflects the energy required by plants to extract water from the soil (Bittelli, 2010), making it a more reliable indicator of soil water availability than soil water content per se.

Due to the limited number of available sensors, soil water potential was monitored in only some of the pots. To overcome this concern, a Soil Water Retention Curve (SWRC) model was built in order to convert soil water content (è) into soil water potential (ø). To this end, soil water potential was measured in three randomly selected pots at two depths; namely 10 and 20 cm. The average of these two measurements was calculated for each pot and paired with the corresponding soil water content. These data were then used to build a predictive model and fit the SWRC.

Generally, SWRCs typically follow a sigmoidal shape (Eyo *et al.*, 2022). In our case, the curve exhibited an asymmetric sigmoidal trend (Fig. 1), which was fitted using a 5-parameter logistic model (Equation 1):

$$\psi = \mathrm{A} + \frac{\mathrm{B} - \mathrm{A}}{(1 + \exp(\mathrm{C} * (\theta - \mathrm{D})))^{G}}$$

..... Equation 1

Where:

A corresponds to the value of the high asymptote; B corresponds to the value of the low asymptote; C corresponds to the slope

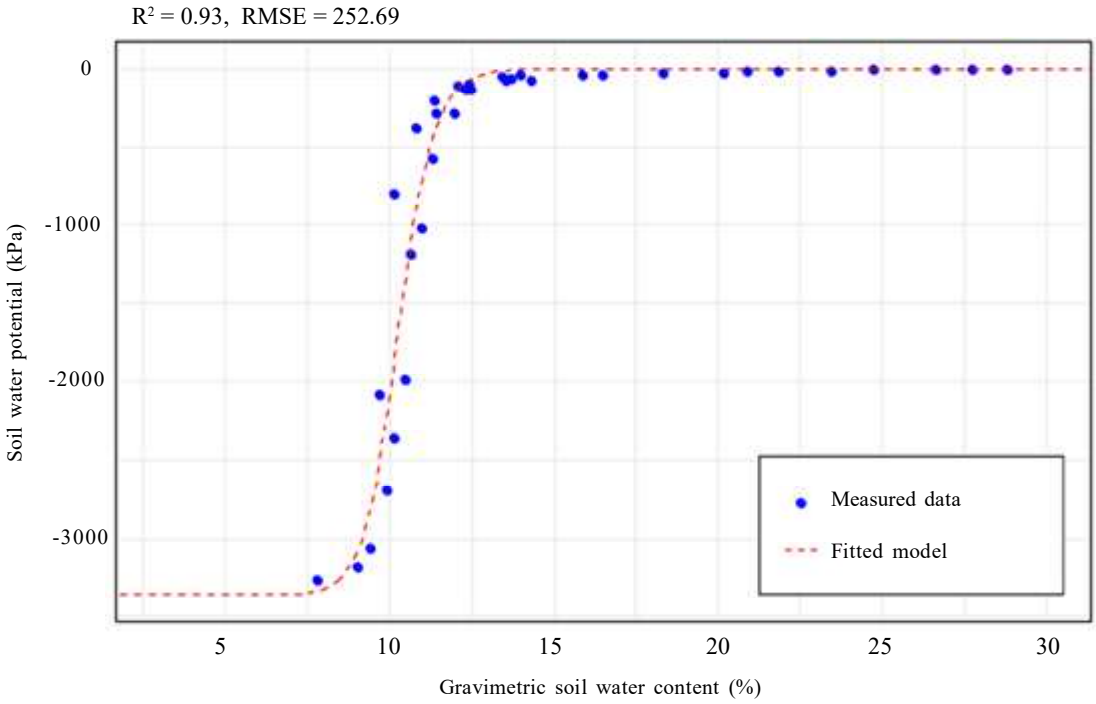


Figure 1. Fitted Soil Water Retention Curve. The coefficient of determination (R2) was calculated as 1-(SSres/SStot), where SSres is the sum of squared residuals and SStot is the total sum of squares. The Root Mean Squared Error (RMSE) was calculated as $\sqrt{(1/n * SSres)}$, where n is the number of observations and SSres is the sum of squared residuals.

around the inflection point, D corresponds to the inflection point and G corresponds to the asymmetry factor. The fitted parameter values were: A = –18.20; B = –3358.69; C = 1.99; D = 10.13 and G = 0.84. The model was fitted in RStudio software (2023.09.1) using the *minpack.lm* package.

**Statistical analyses.** All statistical analyses were performed using RStudio software (2023.09.1). A two-way ANOVA was used to assess the effects of soil water regime and variety on rice biomass parameters (shoot biomass, root biomass, total biomass and shoot:root ratio). A one-way ANOVA was also conducted to determine whether the duration of drought required to reach each stress level differed among varieties. Finally, one-way ANOVA was conducted to assess whether there was a variety effect on changes in soil water content and soil water potential during the drought period.

The normality of the residuals and homogeneity of the variances were checked for each variable, respectively, using the Shapiro–Wilk and Levene's tests. In cases where these assumptions were not met, a Box-Cox transformation was applied to the data. Once the assumptions had been met, the ANOVA was performed. When the ANOVA indicated a significant effect (P-value < 0.05), an LSD post hoc test from the *agricolae* package was used to determine the significance of differences between groups. If the assumptions of the ANOVA were still not met despite transformation, a robust ANOVA from the WRS2 package was used. If the robust ANOVA indicated a significant effect, the *mcp2atm* post hoc test was applied to identify significant differences between groups.

## RESULTS

**Biomass parameters.** All shoot, root and total biomass responded negatively to the effect of drought stress (Fig. 2). The higher was the drought stress level, the lower was the biomass production, with significant differences among soil water regime treatments (Fig. 2, Table 4). At the death stage, shoot biomass was almost reduced to zero because most of the leaves had cracked and fallen off.

On the other hand, neither variety nor interaction between soil water regime and varieties had a significant effect (P>0.05) on shoot, root or total biomass production. Indeed, under each soil water regime, none of the tested varieties differed significantly from the control variety, CD, in terms of biomass production. However, a significant interaction effect was observed on the shoot:root ratio (Table 4). Indeed, soil water regime effect on shoot:root ratio varied depending on the variety. For the control variety, CD, shoot and root biomass production declined in relatively similar proportions, across the soil water regime treatments, resulting in a fairly stable shoot:root ratio (Fig. 2). The same trend was observed for varieties F173, F186 and F200. In contrast, F201 appeared to prioritise maintaining root biomass production under drought conditions. This was particularly evident from the rolling stage to the drying stage, where root biomass production remained virtually constant in F201 (Fig. 2), leading to a lower shoot:root ratio.

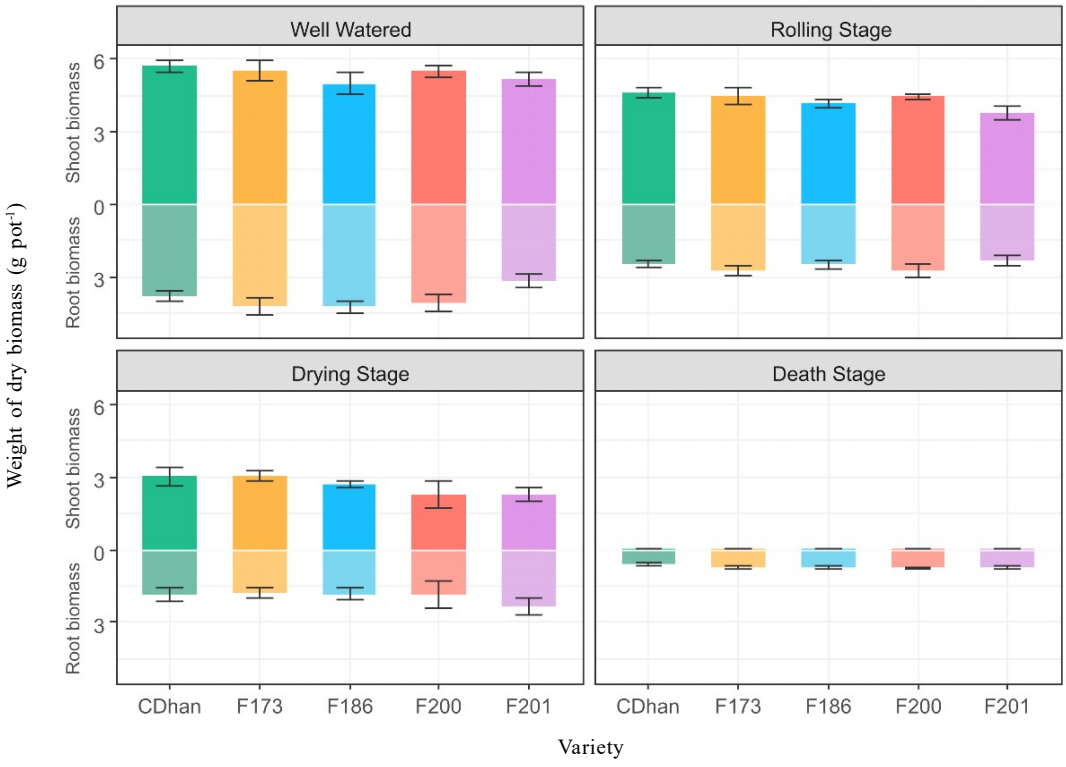


Figure 2. Weight of dry biomass for each variety under the different soil water regimes. Shoot biomass values are repres ented above the horizontal axis and root biomass values are represented below. Error bars indicate standard errors. No significant differences were observed between varieties for each soil water regime.

TABLE 4. ANOVA P-values of main effects (soil water regime and variety) and their interaction on rice biomass parameters

| Rice biomass parameters | Treatments | | |
|---|---|---|---|
| | Soil water regime | Variety | Interaction |
| Shoot biomass | < 0.001 *** | 0.189 | 0.519 |
| Root biomass | < 0.001 *** | 0.596 | 0.202 |
| Total biomass | < 0.001 *** | 0.336 | 0.883 |
| Shoot:root ratio | < 0.001 *** | 0.011 * | 0.004 ** |

**Duration to drought stress levels.** The duration of drought required to reach the different stress levels, varied significantly ($P<0.05$) among the varieties (Fig. 3). At the rolling and the drying stages, a non-sigificant trend was observed; whereby varieties F186 and F201 reached the stress levels later, with a delay of about 2 to 3 days; compared to varieties CD, F173 and F200. Specifically, F186 and F201 reached the rolling stage after around 16 days; while the other three varieties reached it after 13 to 14 days. Similarly, F186 and F201 reached the drying stage after 19 days; while the other three varieties reached it after 16 to 17 days.

At the death stage, the difference between the varieties was not significant, with a P-value slightly above the 0.05 threshold. However, the same trend was observed: F186 and F201 appeared to die later than the other varieties (Fig. 3).

**Soil water content and potential.** The evolution of soil water content, followed a similar trend for all varieties, with a progressive decrease in soil moisture throughout the desiccation period (Fig. 4A). However, a significant varietal effect emerged from the 4$^{th}$ day of desiccation ($P< 0.001$). The rate of soil desiccation began to diverge slightly, leading to noticeable differences in soil moisture levels among the varieties. Indeed, with varieties F186 and F201, the soil maintained slightly higher water content than the other varieties.

The most pronounced difference was observed on the 11$^{th}$ day, where the gravimetric soil water content was approximately 22% for F186 and F201, and around 18% for F173. From the 15$^{th}$ day onwards, the rate of soil desiccation slowed down, and the marked effect of variety disappeared as the soil water content converged toward similarly low moisture levels.

Regarding the evolution of soil water potential (Fig. 4B), values remained close to 0 kPa during the initial phase of desiccation, suggesting that water was still easily accessible to the plants during this period. Soil water potential began to decline slightly from the 14$^{th}$ day of desiccation, before dropping sharply from the 15$^{th}$ day onwards. This sudden drop in soil water potential coincided with the slowdown in the rate of soil desiccation (Fig. 4A). This showed clearly that the plants began to struggle to absorb water from the soil. Furthermore, there was no significant differences ($P > 0.05$) in soil water potential among the varieties throughout the desiccation period. However, although the evolution of soil water potential was similar among the varieties, the fact that stress symptoms appeared later with varieties F186 and F201 (Fig. 3), suggests that they experienced lower water potential values before exhibiting visible signs of drought stress.

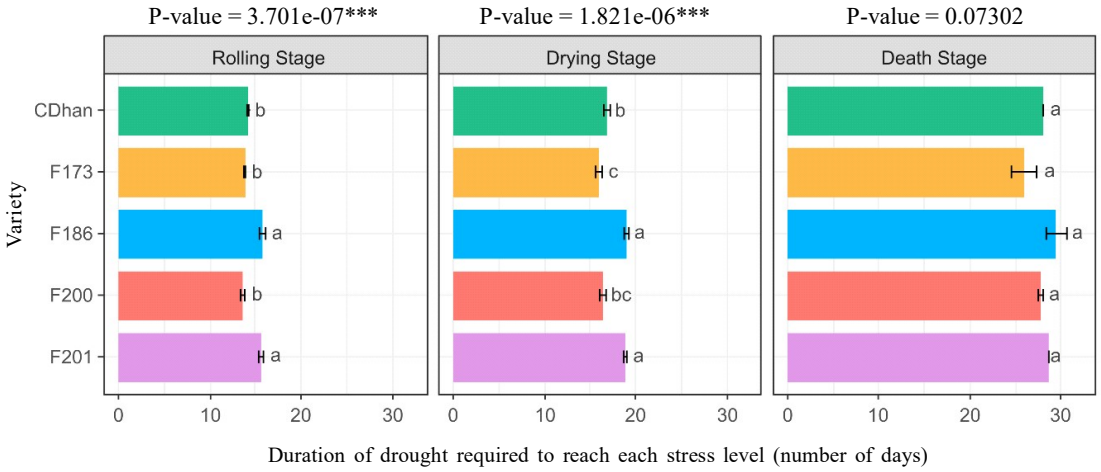


Figure 3. Duration of drought required for each variety to reach the different stress levels. Error bars indicate standard errors. Letters indicate significant differences between varieties at each stress level. The p-value corresponds to the results of the one-way ANOVA assessing the effect of variety within each soil water regime.

## DISCUSSION

**Biomass parameters.** The highly significant negative effect of drought stress on all rice biomass parameters (shoot biomass, root biomass and total biomass) (Fig. 2) is attributed to limited water availability in the soil (Panda *et al.*, 2021), particularly in the first phase of growth when roots systems were insufficient for the function. As a result of this, continuous transpiration induced by the atmosphere (Seleiman *et al.*, 2021; Atta *et al.*, 2022), forced plants to restrict water loss by closing their stomata. This reduced CO, uptake and consequently limits photosynthetic activity (Flexas *et al.*, 2004; Lawlor and Tezara, 2009); consequently causing yield reduction.

Since photosynthesis is the main driver of biomass production in plants, a decrease in photosynthetic activity inevitably slows down, or in cases of severe stress stops biomass production (Männistö *et al.*, 2024; Sun *et al.*, 2024). Beyond the limitation of photosynthesis, the reduction in transpiration caused by drought stress is also detrimental to the uptake and transport of nutrients from the roots to the aerial parts of the plant (Farooq *et al,* 2009; Naik *et al.*, 2022). Transpiration plays an important role in driving the upward movement of water and dissolved nutrients through the xylem. When transpiration is reduced, the flow of nutrients such as nitrogen, phosphorus and potassium is also reduced; thus leading undue nutrient deficiencies in shoot tissues, affecting vital processes such as enzyme activation, protein synthesis and cell division that are essential for plant development and growth (Ciríaco da Silva *et al.*, 2010).

On the other hand, the results showed no significant differences in shoot, root and total biomass between varieties under each soil water regime (Fig. 2). However, a significant interaction effect between soil water regime and variety was observed on the shoot:root ratio (Table 4). This indicates that the changes in carbon allocation strategies between the shoot and root parts, in response to drought stress varied among varieties.

It appeared evident in the presence of drought, that variety F201 had a greater tendency to prioritise root growth, compared to the other varieties. Generally, better root growth is a crucial adaptation strategy for

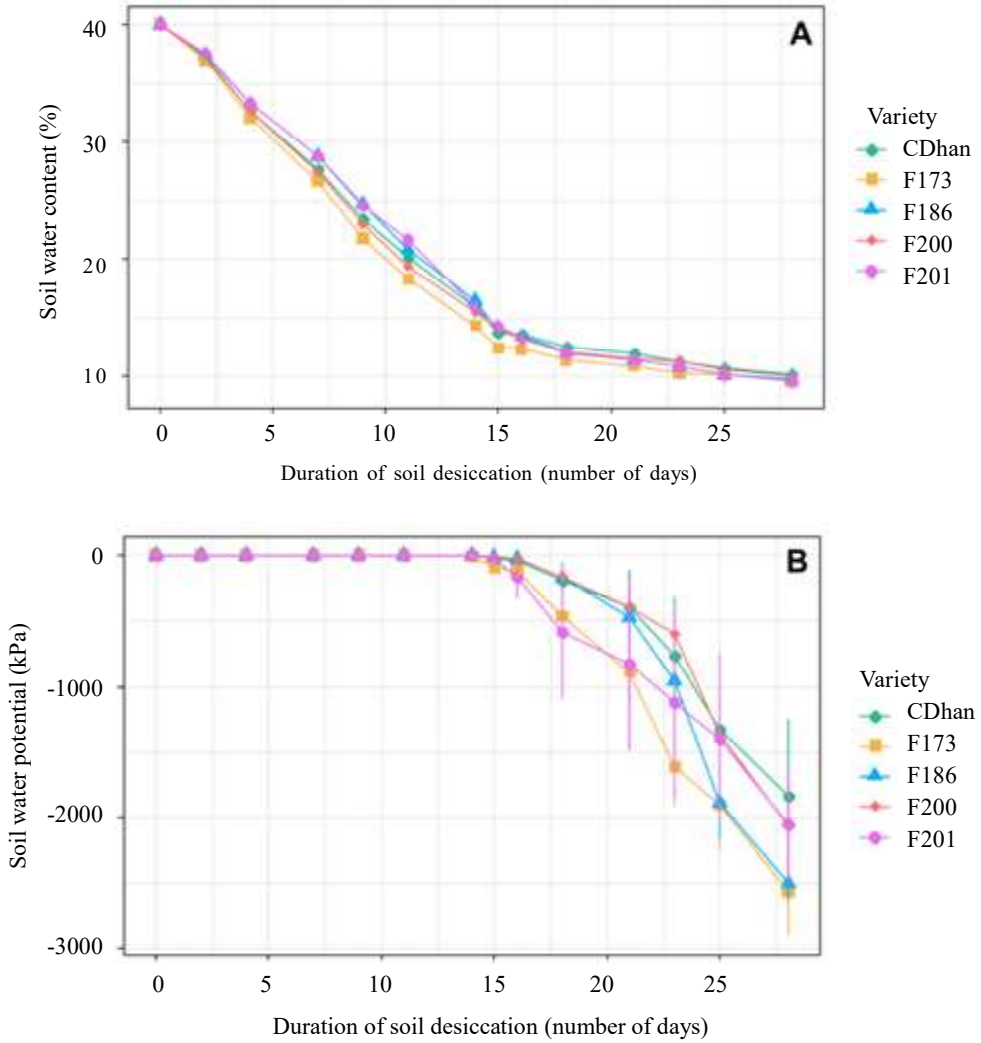


Figure 4. Evolution of soil water content (A) and soil water potential (B) for each variety during the desiccation period. Error bars indicate standard errors.

plants facing water deficit (Kalra *et al.*, 2024); as this allows plants to explore a larger soil volume, increasing water uptake efficiency under limited water regimes (Voothuluru *et al*., 2024).

However, the observed change remained relatively minor as no significant differences were observed in shoot or root biomass individually. Nevertheless, this result highlights potency of a trait that could be targeted for future breeding programmes. It is important to note, however, that the experiment was conducted over a relatively short period, as root growth differences between varieties could potentially become more evident over a longer period.

**Duration to drought stress levels.** It was clear that the duration of drought required to reach the different stress levels varied significantly among the varieties (Fig. 3). In particular, varieties F186 and F201 showed a 2-3 days delay in the onset of drought stress symptoms (leaves rolling and leaves drying),

compared to the other three varieties; and died of later. In Madagascar's Central Highlands, it is common to experience several consecutive days without rainfall, particularly at the beginning of the cropping season. In such a context, the capacity of a variety to endure 2–3 additional days of drought appears to be of sigificant advantage. Moreover, it is important to note that the experiment was conducted under greenhouse conditions, where elevated temperatures can accelerate the soil desiccation and exacerbate drought stress. In real field conditions, where the soil desiccation process may be slower (Baubin *et al*., 2021), these varieties could potentially withstand drought for an even longer period.

**Soil water content and potential.** The delayed onset of drought stress symptoms observed in varieties F186 and F201 can be partially attributed to the slightly higher available soil water levels maintained by these two varieties, during the initial phase of the desiccation period (Fig. 4A). This observed difference in soil water content may be an indication or differing water use strategies among the varieties. F186 and F201, which appeared to slow down soil water depletion, may adopt more conservative water use strategies.

Such behavior is generally associated with physiological traits, such as efficient stomatal regulation or leaf morpho-physiological adaptations that help reduce transpirational water loss (Moshelion, 2020; Yavas *et al.*, 2023). Varieties that limit transpirational water loss, often maintain higher leaf water potentials during soil desiccation (Jarin *et al*., 2024b). As leaf rolling is initiated by the loss of turgor in leaf cells due to a decline in leaf water potential (Ali *et al*., 2022), the fact that F186 and F201 may have transpired less than the other varieties; suggesting that they are able to maintain cell turgor for longer periods, thereby delaying the appearance of visible drought stress symptoms.

In contrast, the other three varieties (CD, F173 and F200) appear to transpire more, making them more rapidly susceptible to an internal water deficit, i.e. a drop in their leaf water potential. This deficit emerges as soon as the rate of transpirational water loss exceeds the capacity of the roots to absorb water from the soil. Figure 4B perfectly illustrates this dynamic; namely leaves rolling for these varieties are observed around the 14$^{th}$ day of desiccation, even though the soil water potential only decreased slightly and remained quite close to 0 kPa. This divergence reveals that these varieties experience an early internal water deficit prior to the notable decrease in soil water potential seen by the 15$^{th}$ day of desiccation.

However, the soil water content alone does not fully explain the delayed onset of drought symptoms, as it its curves converged towards similarly low moisture levels after the 15$^{th}$ of desiccation (Fig. 4A). At this stage, transpiration of all varieties was severely limited, no longer by physiological traits but by the likely critical scarcity of water in the soil. Even the varieties that typically exhibit higher levels of transpiration can no longer extract sufficient water, resulting in a similar transpiration rate across all varieties, as reflected by the uniformly low soil moisture levels. Thus, the dynamics of soil water potential seem to be more informative to explain the delayed appearance of drying stage symptoms in varieties F186 and F201.

Although the overall trend was similar across the varieties, the fact that drought stress symptoms appeared later in F186 and F201 (Fig. 3), suggests that they experienced lower water potentials before exhibiting visible signs. This indicates that there is a difference in physiological tolerance thresholds to water deficit, between varieties. Specifically, F186 and F201 appear to be able to tolerate lower soil water potential values, before exhibiting leaves drying symptoms. This enhanced tolerance can be attributed to various

physiological traits, including osmotic adjustment, cell wall elasticity, or antioxidant defense systems (Jarin *et al.*, 2024b; Li *et al.*, 2024). Thus, although all varieties were exposed to similarly low soil water availability, F186 and F201 emerged with a superior capacity to physiologically adapt prior to succumbing to severe symptoms. This makes them potentially more tolerant under prolonged drought conditions, frequently characteristic of field conditions.

## CONCLUSION

This study has confirmed the hypothesis that, despite the limited genetic diversity of upland rice in Madagascar's Central Highlands, some varieties may exhibit a better tolerance to drought than others. Of the five local varieties tested, two such varieties, F186 and F201, stood out for their delayed expression of drought stress symptoms and extended survival under water deficit conditions. These results highlight significant intraspecific variation in drought response among local germplasm, suggesting that valuable adaptive traits already exist within the rice varieties used in the Central Highlands of Madagascar. Future research under field conditions should aim to better understand the underlying mechanisms that confer this apparent tolerance. In particular, investigations should focus on physiological traits such as stomatal regulation, osmotic adjustment, cell wall elasticity, and antioxidant defense systems, which may play key roles in the drought tolerance observed in these two varieties.

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