Large leaf modulus of elasticity is associated with the distinct midday reduction of photosynthesis in rice (Oryza sativa L.): a comparison with green gram (Vigna radiata (L.) R.Wilczek)

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ABSTRACT

A distinct midday to afternoon (midday) reduction of leaf photosynthetic rate ($A_o$) occurred in rice, even under well-irrigated conditions on a clear day, but not in green gram. No significant differences between species in leaf water potential ($\Psi_{leaf}$) or plant resistance to water transport during daytime were found. From the pressure–volume curves, it was revealed that rice leaves had a larger bulk modulus of elasticity ($\epsilon$), and their turgor pressure ($TP$) decreased more as $\Psi_{leaf}$ declined than of green gram leaves. The $TP$ of rice leaves was estimated to be lower in the midday than that of green gram. We attribute the distinct midday reduction of $A_o$ in rice to the larger $\epsilon$ of rice than that of green gram.

Introduction

World food crop production has more than doubled during the last half century (FAO, 2020). However, additional increases in crop production remain necessary to meet the ever-increasing demands of the rapidly expanding world population. Increasing land area for production is not a sustainable option, and therefore the productivity of existing arable land will have to be improved (Driever et al., 2014). To further improve the yield of grain crops, it is first necessary to understand the characteristics associated with dry matter and grain production in each crop. Leaf photosynthesis is one of the most important physiological processes affecting crop productivity (Fischer & Edmeades, 2010; Gu et al., 2014; Taylaran et al., 2011; Yamori, 2021; Yamori et al., 2016).

A very large reduction in net photosynthetic rate ($A_o$) is often observed in association with water stress during daytime on sunny days (Tazaki et al., 1980).
A similar reduction can also occur during midday to afternoon (midday) even when soil moisture is sufficient (Hirasawa, 2018). Associated with the reduction of $A_n$ under water stress is a reduction of bulk leaf water potential ($\Psi_{leaf}$; Hirasawa, 2018; Kramer & Boyer, 1995). $A_n$ or stomatal conductance ($g_s$) decrease without any detectable reduction of $\Psi_{leaf}$ when atmospheric vapor pressure deficit (VPD) increases or when a part of roots encounters dry soil (Davies & Zhang, 1991; Hirasawa et al., 1988; Salendra et al., 1995). Plants, which have a high resistance to water transport ($R_{plant}$) or encounter a large resistance to water flow from soil to roots, decrease $A_n$ ($g_s$) through the reduction of xylem water potential (Christmann et al., 2007; Hirasawa, 2018; Rodriguez-Dominguez & Brodribb, 2019). In any cases, turgor pressure ($TP$) of the epidermal cells or bulk leaf tissue is associated with the reduction of $A_n$ ($g_s$) under moderate water stress (Buckley, 2019; Christmann et al., 2007; Knipfer et al., 2020; Shackel & Brinckmann, 1985). Leaf TP is influenced by $\Psi_{leaf}$ reduction, solute accumulation and the bulk modulus of elasticity ($\xi$) of the leaf tissue (Kramer, 1983; Kramer & Boyer, 1995; Nadal et al., 2020; Turner, 2018; Tyree & Jarvis, 1982).

Rice (Oryza sativa L.) and pulses such as green gram (Vigna radiata (L.) R. Wilczek), black gram (Vigna mungo (L.) Hepper) and pigeon pea (Cajanus cajan (L.) Millsp) are important food crops in Myanmar and other Southeast Asian countries (FAO, 2020; Kusano & Koyama, 2014). It is well known that rice shows a distinct midday reduction of $A_n$ even in a flooded field (Ishihara & Saito, 1987; Turner et al., 1986). However, the photosynthetic behavior of these pulses has not been revealed. Here, we compared the midday reduction between rice and green gram, focusing on the $\Psi_{leaf}$ reduction, $R_{plant}$ and leaf water characteristics associating to TP.

Materials and methods

Plant materials and cultivation

Myanmar rice cvv. Shwepyihtay and Yeanelo 4 and green gram cvv. Yezin 1, Yezin 11 and Yezin 14 were used in this study. Shwepyihtay and Yeanelo 4 are irrigated rice cultivars with good eating quality. Yezin 1 is indeterminate, and Yezin 11 and Yezin 14 are both determinate.

Seedlings of Yeanelo 4 (3 weeks after sowing) were transplanted into in seven L-pots of sandy loam soil at 3 hills per pot and three plants per hill and grown under flooded conditions. Yezin 1 was grown in 7-L (2018) or 10-L (2019) pots filled with sandy loam soil at 3 hills per pot and at two plants per hill. Basal fertilizer was 0.8 g N, 0.3 g P and 1.0 g K per pot for both species. Pots were placed in the field of Yezin Agricultural University (Yezin, Nay Pyi Taw, Myanmar; 19°76’N, 96°09’E).

Seedlings of both rice cultivars (3 weeks after sowing) were transplanted into a paddy field with sandy loam soil at Yezin Agricultural University at 25 hills m$^{-2}$ (20-cm × 20-cm spacing) with three plants per hill and grown under flooded conditions. Chemical fertilizer was applied at 45.4 kg N, 22.7 kg P and 22.7 kg K ha$^{-1}$ as a basal dressing. The three green gram cultivars were grown under a rain-out shelter in an upland field at Yezin Agricultural University in sandy loam soil at 16.7 hills m$^{-2}$ (30-cm × 20-cm spacing) and grown at 2 plants per hill. Photosynthetically active radiation (PAR) inside the shelter was approximately 80% of that outside. Chemical fertilizer was applied at 30.9 kg N, 30.9 kg P and 30.9 kg K ha$^{-1}$. The two cultivars (rice) or three cultivars (green gram) were arranged in a randomized block design with three replications.

Measurements were made before flowering in late October to November in 2018 and 2019, at the beginning of the dry season in Myanmar, 7 to 8 weeks after sowing of the rice and 4 to 5 weeks after sowing of the green gram. Leaf area of rice plants was similar to that of green gram at the measurements (Table S1).

$A_n$ and $\Psi_{leaf}$

The uppermost fully expanded leaf attached to the main stem and the terminal leaflet of the uppermost fully expanded leaf were used for the measurements in rice and green gram, respectively. $A_n$ and $g_s$ were measured in an open system with a handheld photosynthesis meter (CI-340, CID Bio-Science, Camas, WA, USA). A leaf chamber with window area of 6.25 cm$^2$ (2.5 cm × 2.5 cm) was used. Outside air was pumped into the chamber at 0.2 L min$^{-1}$ for rice or 0.6 L min$^{-1}$ for green gram from a 20-L plastic air bottle. Three 1-min measurements were taken under direct sunlight at ≥1000 μmol m$^{-2}$ s$^{-1}$ PAR.

The $\Psi_{leaf}$ was determined with a pressure chamber instrument (SKPM 1405/40, Skye Instruments, Ltd., Powys, UK). A whole leaf (rice) or a whole terminal leaflet (green gram) was covered with a moistened plastic bag, quickly excised from the plant and installed in the pressure chamber. The inner wall of the pressure chamber was covered with wet filter paper.

To measure diurnal changes in $A_n$ and $\Psi_{leaf}$ of rice, the soil in pots or in the paddy field was kept flooded. For green gram, the soil water potential in pots (at 10 cm) or in the upland field (at 20 cm) was kept at approximately
–6 kPa, as measured with a tensiometer (DM-8, Takemura Electric Works, Ltd., Tokyo, Japan). To examine the \( A_n - \Psi_{\text{leaf}} \) relationship, measurements were taken on the way of the depletion of soil moisture in pots by withholding irrigation.

**Pressure–volume curves**

The pressure–volume curve of the leaves of plants grown in pots was determined as summarized by Boyer (1995) in comparisons of leaf water characteristics (Figure S1). The plants were irrigated well and covered with a black plastic bag overnight to ensure that their leaves were fully turgid. A whole leaf (rice) or a whole terminal leaflet (green gram) was installed in the pressure chamber of the SKPM 1405/40 in the same way as above. A pre-weighed piece of cotton was placed over the exposed cut end, and 0.2 MPa of air pressure was applied for 10 min. The small volume of exuded leaf sap was collected in a cotton, and the cotton was re-weighed to determine the mass of water exuded from the leaf. Then the \( \Psi_{\text{leaf}} \) at the new balance pressure was measured. The pressure was then increased by 0.2 to 0.4 MPa above the last balance pressure, again with collection of the water. This was repeated until the pressure reached approximately 3 MPa. To prevent evaporation during collection, the cotton was enclosed in a plastic bag and the pressure chamber cylinder including the plastic bag +cotton for sap collection was enclosed in a moistened plastic bag. The residual mass of the leaf was quickly weighed after removal from the chamber and excision of the non-pressurized portion. Dry weight was determined after drying the leaf at 80°C for 48 h. The mass of residual water was calculated as the residual mass of the leaf minus dry weight. The collected sap plus residual water was the total water content, i.e. the amount of water contained in the turgid leaf at relative water content (RWC) = 1.0. The RWC at each balance pressure was the water content at that pressure (the total water content – the mass of sap collected to that pressure, inclusive) divided by the total water content. The \( \varepsilon \) of the leaf was calculated in the RWC range when TP was > 0 MPa as (Melkonian et al., 1982; Nadal et al., 2020; Turner et al., 1986):

\[
\varepsilon = \Delta P/\Delta RWC
\]  

where \( P \) is the balance pressure. TP was calculated as the difference between \( \Psi_{\text{leaf}} \) and the osmotic potential in the pressure–volume curve (Figure S1).

\[ \Psi_{\text{soil}} = \Psi_{\text{leaf}} \]  

\[ R_{\text{plant}} \]  

The \( R_{\text{plant}} \) from roots to leaves was determined for plants grown in pots under flooded (rice) or wet soil (green gram) conditions using the following equation:

\[
R_{\text{plant}} = (\Psi_{\text{soil}} - \Psi_{\text{leaf}})/T
\]  

where \( \Psi_{\text{soil}} \) is the water potential of the soil immediately outside the root, and \( T \) is the transpiration rate per leaf area. Since rice was grown in flooded soil and green gram in soil with approximately –6 kPa water potential, \( \Psi_{\text{soil}} \) was high enough relative to \( \Psi_{\text{leaf}} \) to regard \( \Psi_{\text{soil}} \) as 0 MPa for both species (Hirasawa & Ishihara, 1991). To prevent mutual shading, two of the hills were removed from the pot before measurement, and the transpiration rate was determined for one hill per pot from the rate of weight loss of the pot according to Taylaran et al. (2011). All measurements were conducted outdoors on a sunny day for plants with 3.6 to 6.3 mmol m\(^{-2}\) s\(^{-1}\) of transpiration rate. The \( \Psi_{\text{leaf}} \) of the uppermost fully expanded leaf and the third leaf along the stem from that leaf was measured in the equivalent plants growing in different pots.

**Analytical model for \( A_n \) sensitivity**

According to Salvi et al. (2021), a sigmoidal response curve of \( A_n \) to \( \Psi_{\text{leaf}} \) and to TP was fit for the data from each species, and species difference in the response was analyzed using R function ‘SSlogis’ (R core Team, 2021):

\[
A_n = A_{\text{max}} / (1 + \exp[-\beta(x_{\text{mid}} - x)])
\]  

where \( A_{\text{max}} \) is the maximum value of \( A_n \) obtained in the early morning under flooded (rice) or wet soil (green gram), \( \beta \) is a slope coefficient and \( x_{\text{mid}} \) is the \( x \) (\( \Psi_{\text{leaf}} \) or TP) value at which \( A_n \) decreases to half \( A_{\text{max}} \).

**Meteorological data**

Air temperature, VPD and solar PAR data from the routine records of the weather station at the Department of Agricultural Research, Yezin Nay Pyi Taw, adjacent to Yezin Agricultural University, were used in this study.

**Statistical analysis**

The data were analyzed in JMP v.13 software, using a 2-way ANOVA, Student’s t-test, or Tukey–Kramer test of the statistical means, as appropriate. Quadratic regressions between TP, RWC and \( \Psi_{\text{leaf}} \) were fit for data of each species, and intercept and slope differences were determined by ANCOVA in the JMP v.13 software.
Results and discussion

Diurnal changes in \( A_n \) and \( \Psi_{\text{leaf}} \)

The \( A_n \) of the two rice cultivars grown in the flooded paddy field was approximately 23 and 26 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in the morning of a typical clear day (Figure S2A, B). By 13:30 h, \( A_n \) had decreased significantly to approximately 16 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (Figure S2B, inset). In contrast, the three field-grown green gram cultivars showed no significant afternoon reduction of \( A_n \) on a similar warm and bright day (Figure S2C, D).

We compared the diurnal changes in \( A_n \), \( g_s \), and \( \Psi_{\text{leaf}} \) in rice and green gram grown in pots on a same day (Figure 1). In rice, \( A_n \) was 23 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) at 09:00 h but decreased to 15 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) at midday and then to 10 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) at 13:30 h (Figure 1). In green gram, in contrast, \( A_n \) was approximately 28 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) throughout the day, with no afternoon reduction. \( A_n \) was not significantly different between rice and green gram at 10:00 h, but it was significantly smaller in rice in the afternoon. Similar changes were observed in \( g_s \) in both rice and green gram (Figure 1). This suggests that the stomatal limitation caused the midday reduction of \( A_n \) in rice (Hirasawa, 2018).

\( \Psi_{\text{leaf}} \) already decreased to approximately \(-0.7 \text{ MPa} \) at 09:30 h in both species, and by afternoon, it decreased to \(-1.0 \text{ MPa} \) in rice and \(-0.9 \text{ MPa} \) in green gram, although the reduction was not significant (Figure 1). Species difference in \( \Psi_{\text{leaf}} \) also was not significant throughout the day. Since both species showed a higher \( \Psi_{\text{leaf}} \) (approximately \(-0.3 \text{ MPa} \)) compared to the morning of other days, we expect that \( A_n \) started to decrease at 09:00 h in rice. Taken together, the difference in the midday reduction of \( A_n \) between rice and

![Figure 1. Diurnal changes of (A) air temperature, atmospheric vapor pressure deficit (VPD), photosynthetically active radiation (PAR), (B) photosynthetic rate \( A_n \), (C) stomatal conductance \( g_s \) and (D) water potential \( \Psi_{\text{leaf}} \) of uppermost fully expanded leaves in rice and green gram grown in pots on a clear day (18 Nov 2019). A rice cultivar, Yeanelo 4 and a green gram cultivar, Yezin 1 were used for measurements. Bars on symbols represent SE \( (n = 4) \) in B, C and D. Symbols with the same letter do not differ significantly at 5% level in each figure (Tukey HSD test).](image-url)
green gram was not attributable to the difference in the $\Psi_{\text{leaf}}$ reduction, and the response of $A_n$ to $\Psi_{\text{leaf}}$ reduction was more sensitive in rice than in green gram.

**Leaf water characteristics, afternoon TP and $R_{\text{plant}}$**

Rice leaves decreased TP much faster as the RWC declined, and their $\varepsilon$ value was far larger than that of green gram (Figure 2). The TP (or leaf osmotic potential) value at full turgor tended to be lower (higher) in rice, but the species difference was not significant (Figure 2). TP decreased more as $\Psi_{\text{leaf}}$ declined in rice than in green gram, and the TP–$\Psi_{\text{leaf}}$ relationship differed significantly between species (Figure 2).

Although no species difference was found in $\Psi_{\text{leaf}}$, a lower value of TP was estimated in rice than in green gram in the clear day afternoon when the reduction of $A_n$ was remarkable in rice (Figure 3). The $R_{\text{plant}}$ was not different between rice and green gram (Figure 3).

From the results, the species difference in the midday reduction of $A_n$ was not attributable to the difference in $R_{\text{plant}}$ and in soil moisture content; rice and green gram were grown in flooded or adequately wet soil where the resistance to water flow from soil to roots was small enough (Carminati & Javaheris, 2020). Small $\varepsilon$ is thought to facilitate maintenance of cell turgor under water stress (Kramer, 1983; Nadal et al., 2020; Saito & Terashima, 2004; Tyree & Jarvis, 1982). $A_n$ (or $g_n$) reduction under water stress was moderated in the leaves with small value of $\varepsilon$ (Nadal et al., 2021, 2020). Here we revealed that rice had a larger $\varepsilon$, and the TP and $A_n$ of rice decreased more in the midday than those of green gram (Figure 2). Solutes accumulate in leaves during daytime, especially in the afternoon (Turner et al., 1986). We did not consider the daytime accumulation of solutes in the TP estimation (Figure 3). $A_n$ started to decrease in the morning when $\Psi_{\text{leaf}}$ declined in rice as above (Figure 1) and as Turner et al. (1986), Ishihara and Saito (1987), and Taylaran et al. (2011) reported. We expect that the

![Figure 2](image-url). Comparisons of (A) the turgor pressure (TP)—relative water content (RWC) relationship, (B) bulk modulus of elasticity ($\varepsilon$) and (C) the TP–water potential ($\Psi_{\text{leaf}}$) relationship of three uppermost fully expanded leaves between rice (Yeanelo 4; R1, R2, R3) and green gram (Yezin 1; G1, G2, G3) grown in pots (2018). Solid and dotted lines represent quadratic regressions between TP, RWC and $\Psi_{\text{leaf}}$—rice; • green gram. $P$ values in A, C and in B were determined by ANCOVA and Student’s t-test, respectively.

![Figure 3](image-url). Comparisons of (A) photosynthetic rate ($A_n$), (B) water potential ($\Psi_{\text{leaf}}$), (C) turgor pressure (TP) of uppermost fully expanded leaves and (D) plant resistance to water transport ($R_{\text{plant}}$) of uppermost fully expanded leaves between rice (Yeanelo 4, R) and green gram (Yezin 1, G) grown in pots (2018). $A_n$ and $\Psi_{\text{leaf}}$ were measured in the early afternoon on a clear day (Oct. 26). TP was estimated by the regression between TP and $\Psi_{\text{leaf}}$ in Figure 2 (TP) $= 0.376 x (\Psi_{\text{leaf}})^2 + 1.178 x + 0.891$ for rice and $y = 0.227x^2 + 1.043x + 0.981$ for green gram. $R_{\text{plant}}$ was determined on Oct 24. Error bars represent SE ($n = 4$ except for $R_{\text{plant}}$ ($n = 3$)). Symbols indicate significant differences at the *5% and **1% level and ns, not significant at 5% level (Student’s t-test).
difference of the TP and \( A_n \) between rice and green gram emerges in the morning before the significant amount of solutes accumulates in leaves. Thus, we attribute the distinct midday reduction of \( A_n \) in rice to the larger \( \varepsilon \) of rice than that of green gram.

The \( A_n \) of rice decreases without the reduction of \( \Psi_{\text{leaf}} \) when VPD increases (Hirasawa et al., 1988). The increase of VPD may be another cause of the midday reduction of \( A_n \) in rice. When VPD increases, water potential and TP of the epidermal cell decrease due to the increase of leaf transpiration (Mott & Parkhurst, 1991; Shackel & Brinckmann, 1985). The VPD increase may decrease TP of the epidermal cell more in rice leaves with larger \( \varepsilon \) than of green gram even when water potential of their epidermal cell decreases equally.

**\( A_n-\Psi_{\text{leaf}} \) and \( A_n-\text{TP} \) relationships**

We compared the response of \( A_n \) to the \( \Psi_{\text{leaf}} \) reduction when the soil moisture decreased from flooding or field capacity to wilting point. Although rice had a smaller \( \beta \), \( A_n \) decreased quickly when \( \Psi_{\text{leaf}} \) declined and the \( x_{\text{mid}} \) value was higher in rice than in green gram (Figure 4). In contrast with this, no difference in the \( x_{\text{mid}} \) and \( \beta \) between species was observed in the \( A_n-\text{TP} \) relationship (Figure 4). The solute accumulation and increase of the \( \varepsilon \) value were more remarkable under the conditions of long and/or severe water stress (Melkonian et al., 1982; Turner, 2018). We did not consider the solute accumulation and the \( \varepsilon \) value alteration under water stress in the estimation of TP values (Figure 4). The difference in the \( A_n-\Psi_{\text{leaf}} \) relationship between species was more remarkable in the plants under mild (and short) water stress rather than those under severe (and long) water stress (Figure 4). The species difference in the \( A_n-\text{TP} \) relationship was rather small in plants under severe water stress (Figure 4). From the results, the solute accumulation or the \( \varepsilon \) value alteration under water stress might not be a major cause of the difference in the \( A_n \) response between species. It is well known that the \( A_n-\Psi_{\text{leaf}} \) relationship differs among species (Boyer, 1976; Hirasawa, 2018). Our results suggest that the \( \varepsilon \) is associated with the difference in the \( A_n-\Psi_{\text{leaf}} \) relationship between rice and green gram and that \( A_n \) reduction with the decline of \( \Psi_{\text{leaf}} \) is mitigated more in the species with smaller \( \varepsilon \).

A negative relationship between \( A_{\text{max}} \) and \( \varepsilon \) was observed among a wide range of plant species from ferns to angiosperms (Nadal et al., 2018), but \( A_{\text{max}} \) was not different between rice and green gram here even though rice had a larger value of \( \varepsilon \) than of green gram (Figure 1, 4). For other important crops in addition to rice and green gram grown in Myanmar and across Southeast Asia, additional comparative studies of their photosynthetic behavior during the day and under water stress conditions are needed and will improve our understanding on stress tolerance. To obtain a real image of the difference in the photosynthetic behavior among species, investigations of the actual changes in leaf osmotic and cell wall properties in the midday and under soil moisture stress would be required.

**Figure 4.** Relationships between photosynthetic rate (\( A_n \)) and (A) water potential (\( \Psi_{\text{leaf}} \)) and (B) turgor pressure (TP) of uppermost fully expanded leaves in rice (Yeanelo 4; R) and green gram (Yezin 1; G) grown in pots (2019). TP was estimated by the regression between TP and \( \Psi_{\text{leaf}} \) in Figure 2: \( y (\text{TP}) = 0.376 x (\Psi_{\text{leaf}})^2 + 1.178 x + 0.891 \) for rice and \( y = 0.227x^2 + 1.043x + 0.981 \) for green gram. Lines represent sigmoidal fit curves: • rice; ○ green gram. Inserted tables are parameters of the analytical model: \( A_{\text{max}} \), the maximum value of \( A_n \) \((\mu\text{mol} \text{ m}^{-2} \text{ s}^{-1})\); \( x_{\text{mid}} \), the \( \Psi_{\text{leaf}} \) or TP (MPa) at which \( A_n \) decreases to half \( A_{\text{max}} \); \( \beta \), a slope coefficient; \( P \), significant level of the difference between models for rice and green gram on the assumption that rice and green gram have a same \( A_{\text{max}} \) value.
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Disclosure statement

No potential conflict of interest was reported by the authors.

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