Screening New Mungbean Varieties for Terminal Drought Tolerance

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Abstract: Rainfed mungbean crops in Queensland Australia frequently experience terminal drought (drought stress in the final stages of reproductive development), highlighting the importance of drought-tolerant varieties for sustainable mungbean production. Given there is limited information on the relative drought tolerance of current mungbean varieties in Australia, the study of genetic variations and mechanisms of drought tolerance in summer mungbean can provide a basis for developing drought-tolerant mungbean varieties. This study evaluated the physiological, biochemical, and phenological traits underpinning yield attributes associated with drought tolerance in selected mungbean varieties. Four new mungbean varieties (AVTMB#1 to 4) and the Australian commercial line (Jade-AU) were grown in tall (75 cm) polyvinyl chloride (PVC) lysimeters where drought stress was imposed at the early flowering stage (R1) and maintained until maturity. Drought stress significantly impacted all the varieties. Averaged across all the varieties, drought stress was associated with a reduction in stomatal conductance ($g_s$) and photosynthetic rate ($A_{sat}$) by 78% and 86%, respectively, compared to well-watered plants. Internal carbon dioxide concentration ($C_i$), the effective quantum yield of photosystem II ($\Phi_{PSII}$) and maximum light-use efficiency of light-acclimated photosystem II centres ($Fv'/Fm'$) were also decreased, while excitation pressure ($1-q_P$) increased with drought treatment. A positive correlation ($r = 0.60$) existed between seed yield and $\Phi_{PSII}$ assessed at R1, while a weak correlation with $Fv'/Fm'$ ($r = 0.24$) was observed. Excitation pressure ($1-q_P$) at the R1 stage was negatively correlated with seed yield ($r = -0.66$). Therefore, leaf fluorescence measures, viz., $1-q_P$ and $\Phi_{PSII}$, were recommended for use in screening mungbean varieties for drought tolerance. The varieties, AVTMB#1 and AVTMB#4, respectively achieved 39 and 38% greater seed yields relative to the commercial variety, Jade-AU, under terminal drought conditions.

Keywords: pulse; water-use efficiency; photosynthesis; carbon discrimination

1. Introduction

Mungbean [Vigna radiata (L.) Wilczek] is a tropical summer grain legume that is cultivated in Australia from September to October and/or December to January [1]. Temperatures around 30 °C are ideal, and enough rainfall (>30 mm) generally occurs at planting. However, the current average mungbean yield in Australia is less than one ton per hectare, compared to a crop yield potential of 3 t/ha [2,3]. Low mungbean productivity in Australia is due to frequent episodes of crop drought events and a lack of suitable drought-tolerant varieties [3]. Water supply is a major limitation to production, given mungbean cultivation in Australia is predominantly rainfed. Terminal drought stress, or drought stress in the final stages of reproductive development, is widespread because crops are generally planted on low stored soil moisture (90 mm plant-accessible water) with minimal in-crop rain [4]. Cultivation relies on the short duration (90 days) of the crop and the relatively low irrigation needs (3.5–4.5 ML/hectare) [5].

Although mungbean can tolerate mild-to-moderate drought stress during the vegetative and early reproductive stages [6,7], several climate models forecast a rise in drought
frequency [8], posing a key constraint to Australian mungbean cultivation as a rainfed crop in the current mungbean production Australian regions (Queensland and New South Wales) [9,10]. Therefore, an understanding of drought response mechanisms in mungbean is crucial for developing improved and drought-tolerant varieties.

Reduced plant production and growth caused by drought are associated with decreased photosynthetic rates [11], predominantly caused by stomatal closure [12,13], resulting in decreased sucrose production and export from source to sink [14,15]. Gas exchange (photosynthetic rates, stomatal conductance, intrinsic water use), chlorophyll a fluorescence (effective quantum yield of photosystem II (ΦPSII), maximum light-use efficiency of light-acclimated photosystem II (PSII) centres (Fv'/Fm') and increase in excitation pressure (1-qP) have been used as indicators of drought tolerance [16–18].

The change in these indicators under drought stress varies significantly across species and among varieties of a single species [11]. For example, intraspecific variation in drought tolerance has been documented for chickpea [19,20], peanut [21], faba bean [22], soybean [23], cowpea [24], Medicago species [25], rice [26], wheat [27] and cotton [28]. Several studies have demonstrated that mungbean varieties differ in their ability to withstand drought at different phases of growth [29,30]. Drought stress (40% of field capacity) applied during vegetative development reduced mungbean yield by 10–33%, while stress applied during flowering reduced yield by 5–27%, and stress at the early pod filling stage, 53–75%, compared to well-watered plants [4]. Another study reported a 50–60% decrease, with a greater decrease if stress was imposed through the vegetative stage than the reproductive stage [31].

In precursor work, an initial field screening of 25 mungbean varieties grown under optimum growth conditions was carried out in Central and North Queensland, Australia, from 2017 to 2020. From this exercise, four varieties were selected based on their consistently higher seed yield than the current commercially dominant variety, Jade-AU. In the current study, the yield response of these high-yielding varieties was evaluated under drought stress, in comparison to Jade-AU. Additionally, the potential to use leaf gas exchange and chlorophyll a fluorescence measurements obtained before harvest to select for drought-tolerant varieties was evaluated.

2. Materials and Methods
2.1. Plant Material and Growth Conditions

Seed of AVTMB#1 (‘Green Dragon’), AVTMB#2, AVTMB#3, and AVTMB#4 (‘Taipan’) were sourced from Agriventis Technologies Ltd. (Sydney, NSW, Australia) “https://www.agriventis.tech/ assessed on 8 December 2020”. Seeds of Jade-AU were obtained from the Australian Mungbean Association (Dalby, QLD, Australia) “http://www.mungbean.org.au/ assessed on 8 December 2020”.

The experiment was conducted in a glasshouse at Central Queensland University, Rockhampton (23.37° S 150.52° E), Queensland, Australia. The glasshouse temperature during the trial period ranged from 25 to 34 °C and relative humidity ranged from 55 to 65% measured with HOBO Pendant Temp-Light Data Loggers, UA-002-08 (OneTemp, Melbourne, VIC, Australia). Mungbean seeds were sown in polyvinyl chloride (PVC; Holman irrigation pipes, Melbourne, VIC, Australia) lysimeter (15 cm diameter × 75 cm height). A PVC end cap with a diameter of 15.5 cm and 3.5 cm height was fitted at the bottom end of each lysimeter to contain the soil. Four holes (each 5 mm in diameter) were drilled into each PVC end cap to ensure proper drainage. Each lysimeter was lined with a black plastic liner to aid in pulling out the intact root at harvest. Each lysimeter was filled with 6.8 kg of a Premium potting mix with (Searles, Kilcoy, QLD, Australia). The potting mix, as analysed by CSBP Soil and Plant Analysis Laboratory (Perth, WA, Australia), contained on a w/w basis: nitrogen (0.96%), carbon (2.74%), potassium (0.47%), magnesium (0.29%), sodium (0.10%), phosphorus (0.17%), sulphur (0.32%), manganese (290 mg kg⁻¹), zinc (68 mg kg⁻¹), boron (9.5 mg kg⁻¹), copper (1.4 mg kg⁻¹) and iron (104 mg kg⁻¹).
The seeds were surface sterilised by immersing in a 3% \( \text{v/v} \) hydrogen peroxide solution for 5 min followed by rinsing with sterile water. Three seeds were hand-sown per lysimeter at a depth of 2 cm on 11 January 2021 and thinned to one seedling per pot one week after emergence. The combination of lysimeter, potting mix, and plants will collectively be referred to as pots hereafter.

2.2. Experimental Design and Treatments

The trial was laid out in a Completely Randomised Design (CRD) involving five mungbean varieties with two water treatments in six replications, i.e., 30 pots for each water treatment, with a total of 60 pots (Figure 1).

Water holding capacity (WHC) is defined as lysimeter weight with soil at field capacity (FC) minus lysimeter weight with soil at permanent wilting point (PWP). Soil weight at FC was taken after overnight drainage. PWP was determined prior to the experiment by allowing five sample pots containing mungbean plants to dry until a constant weight was achieved. Pots were repositioned every week to accommodate the micro-climatic conditions inside the glasshouse, with a pot-to-pot distance of ~50 cm maintained throughout the trial. Two water treatments were applied: a control treatment (well-watered, ‘WW’ in which soil was maintained at 100% WHC (\( n = 30 \) pots), and (ii) a drought stress, in which water was withheld at 10 days after sowing, with plant water stress apparent by day 37 days after imposition of stress (DAIS), when the soil reached 40% WHC (\( n = 30 \) pots).

At 10 DAS, plants were well established, having reached the second node stage (V2), where the 1st trifoliate leaf was completely expanded and flat and the 2nd trifoliate leaf on the upper node started to unroll [1]. At 37 DAIS, approx. 85% of plants were at R1

Figure 1. Trial set up of five mungbean varieties in lysimeter pots under two water treatments (well-watered and drought stress) in a glasshouse.
(flowering stage, with this soil moisture content maintained until harvesting of the crop at 69 DAS, when 90% of mungbean plants reached maturity, R7 stage [1]).

3. Data Collection

3.1. Plant Water Use and Plant Characters

All pots were weighed twice weekly (on Monday and Thursday) throughout the experiment to assess plant water loss [32]. Days to flowering (DF) and days to maturity (DM) were recorded at 50% flower emergence and 50% of plants achieving physiological maturity, respectively, and presented as days after sowing (DAS).

Pre-dawn leaf water potential (LWP) and leaf area (LA) (cm²) were measured twice during the growing season, firstly at 37 DAS when 85–90% of plants had reached the R1 stage and secondly at 51 DAS when 50% of plants had reached the R5 stage (the beginning of the maturity) [1]. The LWP was measured using a Scholander pressure chamber model 3000-1412 (Soil Moisture Equipment Corp, Goleta, CA, USA) [33]. Pre-dawn water potentials were recorded from the second most fully expanded trifoliate leaf of four plants (n = 4) from each variety and water treatment between 05:00 and 06:30 h. After LWP measurement, the leaf that was sampled for LWP was used to measure leaf area (LA; cm²) using the LeafScan app 2020 Version [34].

3.2. Gas Exchange and Chlorophyll a Fluorescence

Light-adapted chlorophyll a fluorescence and gas exchange parameters were measured weekly and simultaneously using an open gas exchange system with an integrated Fluorometer (Li-6800 Multiphase Flash™ Fluorometer, Portable Photosynthesis System, Li-Cor, Lincoln, NE, USA) from the vegetative stage (V4; 20 DAS) until maturity (R7; 70 DAS when 90% of the pods were mature [1]. The measurements were taken from the topmost fully expanded middle leaflet of a trifoliate leaf. The leaflet was placed carefully in the fluorescence chamber and allowed to adapt to the chamber conditions for 15 min, by which time the photosynthesis rate was steady [35]. Measurements were taken each day from 08:00 to 12:30 h at a cuvette temperature of 25 ºC, a flow rate of 700 µmol s⁻¹, a carbon dioxide concentration of 400 µmol mol⁻¹ and a light intensity of 1500 µmol m⁻² s⁻¹. The time taken for measurement of each leaf was ~10 to 15 min. After recording all parameters, the leaflets were removed from the chamber.

Dark-adapted chlorophyll a fluorescence (Fv/Fm) was determined in situ using a chlorophyll fluorometer (OS-30p; OptiSciences, Hudson, NH, USA). The Fv/Fm ratio represents an estimation of the maximum quantum efficiency of PII reaction centres [36] and ranges from 0.75 to 0.85 for healthy plants. The first measurement of Fv/Fm was made at 9 DAS, prior to withholding water in stressed treatments to set a baseline reading before stress imposition, but the subsequent measurements of Fv/Fm were made on the same day as gas exchange and light-adapted chlorophyll a fluorescence measurement. For the Fv/Fm = (Fm – F0)/Fm measurements, the topmost fully expanded trifoliate leaf from plants (n = 4) of each variety and water treatment was dark-adapted. For dark-adapted leaves (on intact plants), aluminium foil was used and the plants were allowed to adapt to this condition overnight, and Fv/Fm measurements were taken between 06:00 a.m. and 07:00 h on the following morning [36]. The aluminium foil was carefully removed to ensure that no light reached the leaf before the dark-adapted values were recorded.

On each measurement day, gas exchange parameters including light-saturated photosynthetic rates (A sat µmol m⁻² s⁻¹) and stomatal conductance (gs mol m⁻² s⁻¹) were recorded. Intrinsic water-use efficiency (iWUE) was calculated as A sat /gs [37]. Simultaneously, chlorophyll a fluorescence parameters were recorded, including the effective quantum yield of PSII (ΦPSII, representative of the fraction of absorbed light utilised in photochemistry), changes in maximum light-use efficiency of light-adapted photosystem II (PSII) centres (Fv’/Fm’) and photochemical quenching, referred to as qP, which reflects variations in the closing of reaction centres [36]. The relative reduction status of the princi-
pal quinone receptor (QA) of PSII was calculated using the qP values obtained (=1 − qP). 1 − qP is regarded as an indicator of PSII susceptibility to photoinhibition [38,39].

3.3. Relative Chlorophyll Measurement

Leaf chlorophyll content (arbitrary units) was assessed weekly from the V4 stage at 21 DAS until R7 at 69 DAS [1] using a handheld SPAD meter (Minolta, SPAD-502, Tokyo, Japan) on the same leaf used for gas exchange and chlorophyll a fluorescence measurements. Four readings were taken from each plant.

3.4. Dry Matter, Yield Attributes and Water-Use Efficiency

To assess above-ground dry weight (DW), plants were cut at ground level and separated into leaves, stems and pods. Leaves and stems were put into separate paper bags and dried at 65 °C for 72 h. The pods were kept in the glasshouse to dry in sunlight and at ambient temperature, and then seeds were separated from the pods and weighed to record grain yield (g/plant) and 100 seed weight (g). Above-ground biomass (g DW/plant) was determined by combining the dry weights of all above-ground plant parts (stem, leaves and seeds in pods).

To determine below-ground biomass (g DW/plant), the soil within the lysimeter was gently extracted by pulling the liner out of the pot. Roots were gently separated manually from the potting mix and placed on a sieve with a mesh width of 2 mm to avoid root loss. The extracted roots were then gently but thoroughly washed with tap water. Shoot: root ratio was calculated by dividing above-ground biomass (g DW/plant) by below-ground biomass (g DW/plant). Water-use efficiency (g/L) was calculated as the total seed yield (g/plant) divided by total water use by the plant (L) [40].

4. Data Analysis

A repeated measure analysis of variance was performed for gas exchange and chlorophyll a fluorescence parameters measured using “ezANOVA” in R software (R version 4.3.3), considering varieties and water treatment as between-subject factors while time (repeated measurements over seven weeks) as a within-subject factor [41]. Analysis of variance (ANOVA) was performed for a factorial analysis (varieties and water treatment as two independent factors), using statistical software GenStat 19th edition (VSN International, Hemel Hempstead, UK) [42], after testing the data for normality, outliers and homogeneity of error variances, the necessary data transformations (log transformations) were performed, particularly for the yield data. The F ratios were used to note treatment significance (p ≤ 0.05) and mean separation was performed using Tukey HSD [43]. Correlation of coefficient determined by using “corrplot” R package [44,45]. Graphical representation was performed using the R package “ggplot2” [46].

5. Results
5.1. Water Applied

The quantity of water applied to plants of all varieties subjected to drought stress (DS) treatments was approximately 40% of that supplied to the well-watered (WW) treatment (Table 1). There was a significant (p = 0.002) interaction effect between varieties and water treatments, with Jade-AU consuming the highest amount of water in the control treatment. However, all varieties consumed a similar amount of water in the drought stress treatment (Table 1). The daily plant water use (mL per plant per day), for the two irrigation treatments over the different growth stages of the crop, is presented in Figure 2.
Table 1. The volume of water applied (L pot\(^{-1}\)) to mungbean plants in well-watered (WW) and drought stress (DS). The volume of water applied (L pot\(^{-1}\)) to mungbean plants for the drought-stressed (water was withheld on 10 DAS, and 40% water holding capacity ‘WHC’ was maintained for the remaining duration) and well-watered (received 100% WHC, maintained in 3–4 days internal through crop duration) treatments. Data are given as an average ± SE (n = 6). Values with the same letters are not significantly different (p < 0.05). The significant effects are displayed in bold.

<table>
<thead>
<tr>
<th>Mungbean Varieties</th>
<th>Water Applied (L pot(^{-1}))</th>
<th>Water Applied (L pot(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Well-watered</td>
<td>Drought stress</td>
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<tr>
<td>AVTMB-1</td>
<td>15.80 ± 0.72 b</td>
<td>7.97 ± 0.39 a</td>
</tr>
<tr>
<td>AVTMB-2</td>
<td>19.75 ± 1.05 ab</td>
<td>7.85 ± 0.32 a</td>
</tr>
<tr>
<td>AVTMB-3</td>
<td>15.89 ± 1.08 b</td>
<td>8.44 ± 0.30 a</td>
</tr>
<tr>
<td>AVTMB-4</td>
<td>19.26 ± 1.84 ab</td>
<td>8.29 ± 0.53 a</td>
</tr>
<tr>
<td>Jade-AU</td>
<td>21.43 ± 0.79a</td>
<td>7.83 ± 0.39 a</td>
</tr>
</tbody>
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<table>
<thead>
<tr>
<th>F-values</th>
<th>p-values</th>
<th>LSD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Varieties (G)</td>
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<td>0.009</td>
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<td>Treatment (T)</td>
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<tr>
<td>G × T</td>
<td>5.03</td>
<td>0.002</td>
</tr>
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</table>

Figure 2. Time course of water used by five mungbean varieties in two water treatments: Well-watered (WW) = 100% water holding capacity (WHC) and drought stress (DS) = 40% WHC. Data are presented as means ± standard errors (SE) (n = 4 plants). The water in DS treatment was withheld from 10 DAS, with 40% water holding capacity achieved at 37 DAS.

5.2. Water-Use Efficiency

Drought stress altered not just leaf water potentials and leaf area (Table 2), but also water-use efficiency (WUE). WUE (defined as g of seed/L of applied water) in general increased significantly with DS compared to WW treatment. Significant differences in WUE among five mungbean varieties were detected under WW and DS treatments (Figure 3). Variety AVTMB#2 had a higher mean WUE under DS, while variety AVTMB#1 had a higher mean WUE in both watering regimes (Figure 3).
Figure 3. Water-use efficiency (WUE; gL\(^{-1}\)) of five mungbean varieties in two water treatments, Well-watered (WW) = 100% water holding capacity (WHC), drought stress (DS) = 40% WHC. The water in DS treatment was withheld from 10 DAS and 40% WHC was achieved at 37 DAS. Each vertical bar represents mean values (\(n = 6\)) and error bars indicate the standard errors. Letters above vertical bars indicate significant differences among varieties in drought stress and well-watered conditions.

Table 2. Leaf water potential (MPa) at flowering and pod filling stages in five mungbean varieties under two water treatments (well-watered = 100% water holding capacity 'WHC', drought stress = 40% WHC). Values followed by the same letter are not significantly different levels (\(p > 0.05\)). The significant effects are displayed in bold; F and \(p\)-values display no significance. Data are presented as an average ± SE (\(n = 4\)).

<table>
<thead>
<tr>
<th>Varieties</th>
<th>Water Potential (MPa)</th>
<th>Leaf Area (cm(^2))</th>
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<td></td>
<td>Flowering Stage</td>
<td>Pod Filling Stage</td>
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<td>Well-watered</td>
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<td>(-0.74 ± 0.05) a</td>
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<td>AVTMB#4</td>
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<td>Jade-AU</td>
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<td>Drought stress</td>
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<td>Jade-AU</td>
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### Table 2. Cont.

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<td>p-values</td>
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<td>Mean</td>
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<tr>
<td>CV%</td>
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5.3. Leaf Gas Exchange and Chlorophyll a Fluorescence Parameter

Light-saturated photosynthetic rates ($A_{\text{sat}}$) decreased significantly throughout the season, with the decrease greater in DS plants than in WW plants (significant treatment × time effect, Figure 4A; also, Supplementary Data: Table S2). A temporal shift, with respect to treatment, was noted, as the leaf gas exchange changed from the beginning to the end of the season, shown by a decrease in photosynthetic rates by ∼22% in WW plants, whereas they decreased by ∼78% in DS plants. There was also a significant variety × treatment effect ($p = 0.039$, in Figure 4A; also, Supplementary Data: Table S2) with variety AVTMB#3 showing a faster drop in mean photosynthetic rates during the season under drought treatment compared to the other varieties. In addition, Jade-AU exhibited reduced mean photosynthetic rates, particularly under WW conditions.

![Figure 4. Cont.](image-url)
There was also a considerable drop in stomatal conductance throughout the season, particularly in DS plants (significant treatment × time effect, Figure 4B; also, Supplementary Data: Table S2). Between the start and end of the season, stomatal conductance decreased by only ~5% in WW plants but as much as ~86% in DS plants.

The leaf internal carbon concentration (Ci) was maintained throughout the season in WW plants but decreased significantly in DS plants by 48% (significant treatment × time effect, Figure 4B; also, Supplementary data: Table S2). There was also a considerable drop in stomatal conductance throughout the season, particularly in DS plants. The leaf internal carbon concentration (Ci) was maintained throughout the season in WW plants but decreased significantly in DS plants by 48% (significant treatment × time effect, Figure 5B; also, Supplementary Data: Table S2). A significant variety effect was observed ($p = 0.025$), with Jade-AU showing higher mean Ci values mid-season under WW conditions and AVTMB#4 showing a faster decrease in mean Ci particularly under DS.

![Figure 4. Light-saturated photosynthetic rate (Asat; µmol CO₂ m⁻² s⁻¹) — (A) and stomatal conductance (gs; mol H₂O m⁻² s⁻¹) — (B) of five mungbean varieties under well-watered (WW) and drought stress (DS), well-watered (WW = 100% water holding capacity; WHC) and drought stress (DS = 40% WHC). The water in DS treatment was withheld from 10 DAS, and 40% water holding capacity was achieved at 37 DAS. Values are mean (±SE) of $n = 4$ plants and error bars represent standard error. Statistics are reported in Table S2, Supplementary Data.](image1)

![Figure 5. Cont.](image2)
Figure 5. Ci (µmol mol⁻¹)—(A) and iWUE—(B) of five mungbean varieties under well-watered (WW) and drought stress (DS). Leaf internal carbon concentration (Ci, µmol mol⁻¹)—(A) and Intrinsic water use of light-adapted leaves—(B) of five mungbean varieties in two water treatments: well-watered (WW = 100% water holding capacity; WHC) and drought stress (DS = 40% WHC). The water in DS treatment was withheld from 10 DAS, and 40% water holding capacity was achieved at 37 DAS. Values are mean (±SE) of n = 4 plants and error bars represent standard error. Statistics are reported in; Supplementary Data: Table S2.

Across the season, iWUE was significantly increased by ~9% in WW plants, and by ~67% in DS plants (significant Treatment × Time effect, p < 0.001, Figure 5B; also, Supplementary Data: Table S2).

The effective quantum yield of photosystem II (ΦPSII) decreased significantly over the growing period, and the decrease was greater in DS plants than in WW plants (significant Treatment × Time effect, Figure 6A; also, Supplementary Data: Table S2). In detail, a considerable drop in ΦPSII over the growing period was observed with a decline of ~28% in WW plants and ~56% in DS plants. There was also a significant variety x treatment effect (p = 0.001, Figure 6A; also, Supplementary Data: Table S2), with AVTMB#3 showing a faster decline in mean ΦPSII than the other varieties under DS, while Jade-AU showed a considerable decline in mean ΦPSII under WW conditions.

The maximum light-use efficiency of light-acclimated photosystem II (PSII) centres (Fv'/Fm') decreased throughout the growing period, and the decrease was greater in DS plants compared to WW plants (significant Treatment × Time effect, Figure 6B; also, Supplementary Data: Table S2). Fv'/Fm' dropped over the growing period by only ~3% in WW plants but ~22% in DS plants (Figure 6B; also, Supplementary Data: Table S2).

Fv/Fm dropped throughout the season, particularly in DS plants (significant Treatment × Time effect, Figure 7A; also, Supplementary Data: Table S2). From the start to the end of the season, Fv/Fm decreased by only ~3% in DS plants. Moreover, there was no intra-specific genotypic variability (Figure 7A; also, Supplementary Data: Table S2). Excitation pressure (1-qP) increased significantly over the growing period, and in DS plants, compared to the WW treatment (significant Treatment × Time effect, Figure 7B; also, Supplementary Data: Table S2). Over the growing period, 1-qP increased by ~29% in WW plants, whereas increased by ~38% in DS plants. There was also a varietal difference with Jade-AU showing the steepest increase in mean excitation pressure, particularly under WW conditions and AVTMB#3 showing the steepest increase (21%) under DS plants (Figure 7B; also, Supplementary Data: Table S2).
Figure 6. PhiPS2 (ΦPSII)—(A) and Fv'/Fm'—(B) of five mungbean varieties under well-watered (WW) and drought stress (DS). Light accounted for photochemistry PSII (ΦPSII)—(A) and photochemical efficiency of open PSII centres in light-adapted leaves Fv'/Fm'—(B) of five mungbean varieties in two water treatments: well-watered (WW = 100% water holding capacity; WHC) and drought stress (DS = 40% WHC). The water in DS treatment was withheld from 10 DAS, and 40% water holding capacity was achieved at 37 DAS. Values are mean of n = 4 plants with associated error bars representing standard error. Statistics are reported in Table S2, Supplementary Data.
Figure 7. Fv/Fm—(A) and 1-qP)—(B) of five mungbean varieties under well-watered (WW) and drought stress (DS). Quantum yield efficiency of dark-adapted leaves (Fv/Fm)—(A) and excitation pressure (1-qP)—(B) of five mungbean varieties in two water treatments: well-watered (WW = 100% WHC) and drought stress (DS = 40% WHC). The water in DS treatment was withheld from 10 DAS, and 40% water holding capacity achieved at 37 DAS. Values are mean (±SE) of n = 4 plants and error bars represent standard error. Statistics are reported in Table S2, Supplementary Data.
5.4. Leaf Chlorophyll Content

The leaf chlorophyll content (SPAD units) remained in the range of 40–55 over the trial period and across both watering regimes, and there was no significant difference between tested varieties, (Figure 8; also, Supplementary Data: Table S2).

Figure 8. Leaf chlorophyll content (SPAD units) of five mungbean varieties under well-watered (WW = 100% WHC) and drought stress (DS = 40% WHC). The water in DS treatment was withheld from 10 DAS and 40% water holding capacity was achieved at 37 DAS. Values are mean (±SE) of $n = 4$ plants and error bars represent standard error. Statistics are reported in Table S2, Supplementary Data.

5.5. Dry Matter Production

There was a significant ($p < 0.001$) variety × water treatment interaction for leaf count (LC; #/plant), stem weight (g DW/plant) and above-biomass weight (g DW/plant), suggesting that varieties responded differently to the two water regimes (Table 3). DS reduced LC and stem DW by 25% and 73%, respectively, relative to WW plants, with Jade-AU experiencing the largest drop in both parameters (LC and stem DW) under DS compared to other varieties (Table 3). Drought caused a 57% decrease in above-ground biomass (g DW/plant) with Jade-AU exhibiting the lowest mean above-ground biomass in DS compared to other varieties (Table 3). However, DS dramatically reduced plant height (cm) by 20%, leaf DW by 73%, and root biomass (g DW/plant) by 63%, with an increase in the root: shoot ratio. However, plant height, leaf DW, root biomass and root: shoot ratio did not show any genotypic variation or interaction effect.
Table 3. Statistical summary of growth, dry weights, and yield parameters at harvest in five mungbean varieties under well-watered (WW) and drought stress (DS).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>AVTM#1 WW</th>
<th>AVTM#1 DS</th>
<th>AVTM#2 WW</th>
<th>AVTM#2 DS</th>
<th>AVTM#3 WW</th>
<th>AVTM#3 DS</th>
<th>AVTM#4 WW</th>
<th>AVTM#4 DS</th>
<th>Jade-AU</th>
<th>p-Values, (LSD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>YLD</td>
<td>19.67 ± 1.56</td>
<td>6.83 ± 1.20</td>
<td>24.87 ± 3.23</td>
<td>6.13 ± 0.61</td>
<td>16.13 ± 2.96</td>
<td>6.12 ± 0.88</td>
<td>22.57 ± 3.58</td>
<td>7.68 ± 0.90</td>
<td>21.20 ± 2.21</td>
<td>5.32 ± 0.67</td>
</tr>
<tr>
<td>Log YLD</td>
<td>1.31 cd</td>
<td>0.89 b</td>
<td>1.39 d</td>
<td>0.80 ab</td>
<td>1.21 c</td>
<td>0.84 ab</td>
<td>1.34 cd</td>
<td>0.87 b</td>
<td>1.33 cd</td>
<td>0.70 a</td>
</tr>
<tr>
<td>HI</td>
<td>0.33 ± 0.02</td>
<td>0.35 ± 0.05</td>
<td>0.33 ± 0.03</td>
<td>0.32 ± 0.02</td>
<td>0.30 ± 0.03</td>
<td>0.33 ± 0.03</td>
<td>0.32 ± 0.04</td>
<td>0.32 ± 0.02</td>
<td>0.28 ± 0.02</td>
<td>0.28 ± 0.03</td>
</tr>
<tr>
<td>Log HI</td>
<td>0.12 ab</td>
<td>0.14 a</td>
<td>0.12 ab</td>
<td>0.18 Ab</td>
<td>0.11 ab</td>
<td>0.12 ab</td>
<td>0.12 Ab</td>
<td>0.13 ab</td>
<td>0.10 ab</td>
<td>0.11 a</td>
</tr>
<tr>
<td>AGB</td>
<td>59.63 ± 4.50</td>
<td>20.61 ± 2.95</td>
<td>74.70 ± 6.03</td>
<td>19.15 ± 1.09</td>
<td>55.19 ± 7.71</td>
<td>23.94 ± 2.18</td>
<td>71.28 ± 5.71</td>
<td>24.36 ± 2.44</td>
<td>75.60 ± 2.78</td>
<td>19.20 ± 0.59</td>
</tr>
<tr>
<td>Log AGB</td>
<td>1.78 cd</td>
<td>1.30 b</td>
<td>1.87 de</td>
<td>1.26 ab</td>
<td>1.72 c</td>
<td>1.29 b</td>
<td>1.85 de</td>
<td>1.30 b</td>
<td>1.88 e</td>
<td>1.16 a</td>
</tr>
<tr>
<td>RB</td>
<td>5.16 ± 0.55</td>
<td>2.15 ± 0.16</td>
<td>6.01 ± 0.51</td>
<td>2.24 ± 0.10</td>
<td>4.75 ± 0.72</td>
<td>2.77 ± 0.27</td>
<td>6.13 ± 0.91</td>
<td>2.76 ± 0.20</td>
<td>6.19 ± 0.58</td>
<td>2.22 ± 0.13</td>
</tr>
<tr>
<td>Log RB</td>
<td>0.78 c</td>
<td>0.43 ab</td>
<td>0.83 c</td>
<td>0.47 ab</td>
<td>0.74 c</td>
<td>0.54 b</td>
<td>0.83 c</td>
<td>0.48 ab</td>
<td>0.84 c</td>
<td>0.41 a</td>
</tr>
<tr>
<td>R:S</td>
<td>0.09 ± 0.01</td>
<td>0.12 ± 0.02</td>
<td>0.08 ± 0.01</td>
<td>0.12 ± 0.01</td>
<td>0.09 ± 0.01</td>
<td>0.12 ± 0.01</td>
<td>0.09 ± 0.01</td>
<td>0.12 ± 0.01</td>
<td>0.08 ± 0.01</td>
<td>0.12 ± 0.01</td>
</tr>
<tr>
<td>Log R:S</td>
<td>0.06 a</td>
<td>0.03 ab</td>
<td>0.03 a</td>
<td>0.04 bcd</td>
<td>0.04 a</td>
<td>0.06 d</td>
<td>0.03 a</td>
<td>0.04 abc</td>
<td>0.03 a</td>
<td>0.05 cd</td>
</tr>
<tr>
<td>PDW</td>
<td>28.18 ± 2.12</td>
<td>8.26 ± 1.64</td>
<td>35.39 ± 4.20</td>
<td>8.11 ± 0.77</td>
<td>23.58 ± 4.11</td>
<td>10.17 ± 1.12</td>
<td>31.47 ± 4.14</td>
<td>10.25 ± 1.17</td>
<td>31.66 ± 2.83</td>
<td>6.57 ± 0.61</td>
</tr>
<tr>
<td>Log PDW</td>
<td>1.46 cd</td>
<td>0.97 a</td>
<td>1.54 d</td>
<td>0.90 ab</td>
<td>1.36 c</td>
<td>0.93 b</td>
<td>1.49 d</td>
<td>0.98 b</td>
<td>1.50 d</td>
<td>0.79 a</td>
</tr>
<tr>
<td>SDW</td>
<td>12.6 ± 1.3 a</td>
<td>4.8 ± 0.6 a</td>
<td>15.8 ± 1.3 ab</td>
<td>4.1 ± 0.1 a</td>
<td>13.3 ± 1.5 ab</td>
<td>5.3 ± 0.8 a</td>
<td>15.8 ± 1.4 ab</td>
<td>5.6 ± 0.9 a</td>
<td>18.5 ± 0.4 b</td>
<td>4.7 ± 0.3 a</td>
</tr>
<tr>
<td>Log SDW</td>
<td>1.12 c</td>
<td>0.71 b</td>
<td>1.22 cd</td>
<td>0.69 ab</td>
<td>1.14 c</td>
<td>0.69 ab</td>
<td>1.21 cd</td>
<td>0.70 b</td>
<td>1.28 d</td>
<td>0.59 a</td>
</tr>
<tr>
<td>LDW</td>
<td>13.66 ± 1.53</td>
<td>5.32 ± 0.67</td>
<td>17.41 ± 1.79</td>
<td>4.72 ± 0.26</td>
<td>13.49 ± 2.01</td>
<td>5.63 ± 0.75</td>
<td>17.88 ± 1.78</td>
<td>5.67 ± 0.63</td>
<td>19.26 ± 0.93</td>
<td>5.65 ± 0.40</td>
</tr>
<tr>
<td>Log LDW</td>
<td>1.15 b</td>
<td>0.74 a</td>
<td>1.25 bc</td>
<td>0.73 a</td>
<td>1.13 b</td>
<td>0.69 a</td>
<td>1.26 bc</td>
<td>0.72 a</td>
<td>1.30 c</td>
<td>0.66 a</td>
</tr>
<tr>
<td>PH</td>
<td>56 ± 0.42</td>
<td>47 ± 3.72</td>
<td>56 ± 9.16</td>
<td>45 ± 9.25</td>
<td>59 ± 6.00</td>
<td>43 ± 2.11</td>
<td>56 ± 4.96</td>
<td>45 ± 2.67</td>
<td>56 ± 4.07</td>
<td>46 ± 5.80</td>
</tr>
<tr>
<td>Log PH</td>
<td>1.75 b</td>
<td>1.68 a</td>
<td>1.74 b</td>
<td>1.65 a</td>
<td>1.77 b</td>
<td>1.64 a</td>
<td>1.75 b</td>
<td>1.65 a</td>
<td>1.75 b</td>
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<tr>
<td>LC</td>
<td>20 ± 1.60</td>
<td>11 ± 1.64</td>
<td>25 ± 2.16</td>
<td>9 ± 0.98</td>
<td>19 ± 2.88</td>
<td>12 ± 1.40</td>
<td>24 ± 2.07</td>
<td>10 ± 1.32</td>
<td>23 ± 0.92</td>
<td>8 ± 0.82</td>
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<tr>
<td>Log LC</td>
<td>1.32 cd</td>
<td>1.04 b</td>
<td>1.40 d</td>
<td>1.00 ab</td>
<td>1.28 b</td>
<td>1.09 b</td>
<td>1.39 cd</td>
<td>1.02 ab</td>
<td>1.37 cd</td>
<td>0.93 a</td>
</tr>
</tbody>
</table>

Note: Abbreviations were used where G represents varieties, Trt represents treatments. Log word with the parameters showed the log-transformed data of those specific parameters.
5.6. Yield Attributes and Yield

Across all varieties, drought stress was associated with a 61% decrease in pod DW (significant variety × treatment effect, \( p = 0.012 \)) (Table 3). Overall, drought significantly reduced seed yield (~71%) while representing a significant interaction effect between water treatment × variety revealed differences among five mungbean varieties for their drought response (Table 3). The seed yield between the varieties in WW conditions was not significantly different, but the reduction in seed yield in the drought treatment was significantly higher in Jade-AU compared to AgriVentis mungbean AVTMB#1 and AVTMB#4. Seed size is one of the critical yield determinants of the mungbean crop. In the present investigation with DS, total seed yield was affected, although seed size did not decrease as a result of reduced water application.

5.7. Seed Yield

Under the drought treatment, AgriVentis line AVTMB#1 and AVTMB#4 produced the higher seed yield; however, AgriVentis variety AVTMB#3 had the lowest drop in relative seed yield, which may be ascribed to the fact that variety AVTMB#3 did not perform as high as other AVT lines in the WW treatment. AVTMB#1 and AVTMB#4 had the lowest relative yield loss in the DS condition (Figure 9).

Figure 9. Seed yield (g plant\(^{-1}\)) of five mungbean varieties in two water treatments, well-watered (WW) = 100% water holding capacity (WHC), drought stress (DS) = 40% WHC. The water in DS treatment was withheld from 10 DAS and 40% WHC was achieved at 37 DAS. Each vertical bar represents mean values (\( n = 4 \)) and error bars indicate the standard errors.

6. Discussion

6.1. Water Potential

Leaf water potential provides an indicator of crop drought stress avoidance when measured 7 days after drought stress imposition at the anthesis stage [47]. All varieties decreased stomatal conductance at the flowering stage, resulting in leaf water potential values close to that of WW plants, suggesting an isohydric mechanism of stomatal control under DS. By the pod-filling stage, the water potential of DS plants had decreased relative to WW plants, as expected.

LWP is regarded as a crucial physiological trait for drought tolerance, with tolerant varieties tending to maintain a higher LWP under stress conditions. The strategy of
maintaining a higher LWP during drought conditions is referred to as a drought avoidance strategy. At the flowering stage, variety Jade-AU maintained higher LWP in WW while dropping considerably under drought (−0.50 in WW vs. −0.84 in DS) while variety AVTMB#1 maintained higher LWP in both water regimes compared to other varieties (−0.58 in WW vs. −0.76 in DS) at pod filling stage. Overall, among these varieties, AVTMB#1 maintained the highest LWP (MPa) at flowering (−0.75 in WW vs. −0.78 in DS). This could be explained by strong stomatal regulation under drought stress response for stomatal closure to save water loss. The pronounced drop in water potential, to as low as −1.06 MPa, in Jade-AU, at the pod filling stage, was associated with a decrease in stomatal conductance (below 100–50 H₂O mmol m⁻² s⁻¹). Drought stress restricts water supply and decreases leaf water content and water potential, resulting in decreased turgor, stomatal conductance and photosynthesis, and a subsequent decline in grain yield [48]. Numerous studies have shown that drought-tolerant varieties maintained a higher LWP despite a water deficit [49], and the present study is consistent with earlier research indicating that the tolerant variety AVTMB#1 maintained a higher LWP under stress.

6.2. Crop Phenology

In the present study tolerant varieties (AVTMB#1 and AVTMB#4) achieved 50% flowering and maturity earlier in drought treatment than other varieties. This is a drought escape strategy, characterised by shorter duration (early maturity) plant growth and development to complete the life cycle before the beginning of the drought [50,51]. This could be a drought tolerance strategy in plants reported in many crops [51,52].

6.3. Effects of Drought Stress on Gas Exchange

Plant regulation of stomatal conductance plays a critical role in drought adaptation [53,54]. In the present study, a positive correlation existed between overall stomatal conductance in drought stress treatment and seed yield measured from the V4 (20 DAS) to R7 (70 DAS) stages. Under drought stress, the photosynthetic rate and stomatal conductance were decreased. Mungbean plants in drought stress (40% WHC) showed a substantial decrease in A sat and g s 28 days after stress application. According to Flex et al. (2006), g s below 100 H₂O is a sign of extreme drought stress in plants [54]. However, g s alone is not a reliable indicator of drought stress as it may vary between varieties and does not account for the length of the drought stress. The g s fell below 100 mmol H₂O in AVTMB#2 and AVTMB#3 after 45 days of stress imposition and in Jade-AU after 53 days, but this did not occur in AVTMB#1 and AVTMB#4 until after 60 days of stress imposition.

To deal with drought stress, plants employ two distinct stomatal conductance strategies: isohydry and anisohydry. Stomatal closure is used by isohydic species to preserve daytime leaf water relations that are unaffected by drought stress. By contrast, anisohydic species may endure greater water losses and extremely low water potentials during drought, a pattern that is frequently associated with less sensitive stomatal regulation. In the present study, stomatal conductance decreased by 55% under DS, and a substantial reduction in pre-dawn water potential was observed at both stages, which represents an anisohydric strategy.

The pre-dawn water potentials of plants in the drought stress treatment dropped to as low as −1.06 MPa when g s fell below 100 mmol H₂O. The decline in A sat could be solely due to the decrease in stomatal conductance, or also due to metabolic impairment of photosynthesis [55]. A sat and seed yield were shown to be positively correlated in this study. Reduced stomatal conductance and A sat were shown to be linked with lower Ci in both drought stress treatments in the current research. Ci reduction is mostly due to stomatal constraints since active photosynthetic machinery depletes CO₂ inside the leaves [56,57]. Initially, Ci remained stable but as drought stress progressed, Ci decreased, pointing towards metabolic impairment of photosynthesis [16].
6.4. Effects of Drought Stress on Chlorophyll a Fluorescence

A photosystem under stress has excess excitation energy, indexed by a variety of chlorophyll a fluorescence parameters [36]. Water limitation was associated with a lower effective quantum yield of PSII (Φ_{PSII}) demonstrating that photochemistry conversion capacity and linear electron flow were both responsive to the severity and duration of drought stress [58]. Also, Φ_{PSII} and seed yield were highly correlated under drought stress in the present trial.

Fv/Fm, the maximum quantum yield for primary photochemistry (Fv/Fm), may be used to quickly and easily determine if plants have been subjected to stress [59,60]. Fv/Fm was not significantly affected by DS plants, suggesting that reliance on this parameter alone could not accurately reflect relative tolerance under drought studies [61]. A significant increase in excitation pressure (1-qP) was also observed. High excitation pressure is associated with excessive energy fluxes, likely to result in photodamage to plants [16]. A strong correlation was observed between 1-qP (averaged across all varieties, in DS treatment) and seed yield.

6.5. Effect of Drought on Growth, Yield and Morphological Parameters

All the growth and yield components were strongly impacted by drought stress in the present study. The leaf area decreased with drought stress in one of the drought-tolerant varieties (AVTMB#4), which is in agreement with earlier studies by Ranawake et al. (2011) [62]. Leaf area is directly related to the final dry matter weight of shoots. This is a drought-avoiding mechanism because decreasing the leaf area results in less water loss through transpiration [63]. The reduction in leaf area is most likely due to the inhibition of leaf expansion caused by reduced cell division due to cell turgor loss [64]. Severe drought also impairs mitosis, causing poor growth [65]. Varieties AVTMB#1 and AVTMB#4 produced significantly higher seed yields under DS treatment. The above-ground biomass under drought stress was higher in variety AVTMB#4 than in the remaining varieties. The higher seed yield was associated with a higher pod dry weight. However, no significant differences were observed in terms of harvest index.

6.6. Correlation Analysis

Gas exchange and chlorophyll a fluorescence parameters were measured at 37 days of stress application (DS; 40% WHC) while yield-related parameters were recorded at harvest. Correlations among the gas exchange, chlorophyll a fluorescence and yield-related parameters were observed (Figure 10). Of all measured parameters, the strongest relationship with yield (YLD) was found with 1-qP (r = −0.66) and Φ_{PSII} (r = 0.60), a moderate positive for A_{sat} (0.49) and g_s (0.33) existed; however, a weak correlation (0.24) was noted between YLD and Fv′/Fm′ (Figure 10).
7. Conclusions

There was no significant yield difference between the five varieties under well-watered conditions; however, AVTMB#1 and AVTMB#4 outperformed other varieties including Jade-AU under drought stress. These lines were therefore recommended for further evaluation in rainfed production systems in northern Australia and have been adopted by growers for large-scale commercial production in Queensland as a rainfed crop. These two lines also showed great water-use efficiencies underpinned by a lower yield penalty under drought treatment compared to the well-watered plants. Various leaf gas exchange parameters were also found to correlate with seed yield under drought treatment. However, leaf chlorophyll a fluorescence parameters, viz., $1-qP$, and $\Phi_{PSII}$, were strongly associated with physiological adaptations conferring a greater LWP, and leaf area under water stress conditions. These traits could also aid in indirect selection and screening tools for drought tolerance of mungbean for improved drought tolerance in new varieties.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agriculture14081328/s1. Table S1. The details about line ID, progeny, and country of four AgriVentis mungbean varieties selected for the screening of drought, waterlogging and Mn tolerance at the flowering, pod filling and seedlings stages, respectively. Table S2. Gas exchange ($A_{sat}$, $gs$, $Ci$, iWUE, $\Phi_{PSII}$ (PhiPS2), $Fv'/Fm'$, $Fv/Fm$, $1-qP$), leaf chlorophyll contents (SPAD units), leaf count (LC; #/plant), plant height (PH; cm), leaf dry weight (LDW; g DW/plant), stem dry weight (PDW; g DW/plant), above-ground biomass (AGB; g DW/plant), root biomass (RB; g DW/plant), root:shoot ratio (R:S), seed yield (YLD; g/plant), 100-seed weight (100SW; g), and harvest index (HI) at flowering stage 37 DAS in drought stress (40% WHC) treatment.
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pressure (1-qP) and leaf chlorophyll contents (SPAD values) of five mungbean varieties, one representing widely grown commercial variety Jade-AU and four Agriventis varieties (AVTMB#1, AVTMB#2, AVTMB#3 and AVTMB#4). The parameters were observed in repeated measure analysis of variance (ANOVA) under two water treatments (Well-watered = 100%WHC, Drought stress = 40%WHC), by considering varieties and treatment as between-subject factors and time (DAS) as a within-subject factor (significant results represented with $p < 0.05$). Abbreviations were used as G = Varieties, Trt = Treatment, Ti = Time. Table S3. Days to 50% flowering and maturity in five mungbean varieties (AVTMB#1, AVTMB#2, AVTMB#3 and AVTMB#4 along with Jade-AU) under two water treatments (well-watered=100%WHC, drought stress = 40%WHC). In drought stress reduction in days to achieve 50% flowering and maturity are shown in parenthesis (with a minus sign). Data is an average of four replications ($n = 4 \pm SE$). Same letters display no significance while different letters display significant effects.

Author Contributions: Conceptualization, S.I., S.B. and K.B.W.; methodology, S.I., S.B. and K.B.W.; software, S.I.; validation, S.I., S.B. and K.B.W.; formal analysis, S.I. and S.B.; investigation, S.I.; data curation, S.I.; writing—original draft preparation, S.I.; writing—review and editing, S.I., S.B. and K.B.W.; visualization, S.I. and S.B.; supervision, S.B. and K.B.W.; project administration, S.B.; funding acquisition, S.I. and S.B. All authors have read and agreed to the published version of the manuscript.

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