

**EFFECTS OF WATER STRESS ON WATER USE EFFICIENCY OF DIFFERENT VARIETIES OF COMMON BEAN (*PHASEOLUS VULGARIS* L.).**

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**Abstract:** Increasing water use efficiency (WUE), which is defined as the biomass increase per unit of water transpired, is a promising avenue for crop yield improvement, especially in drought-prone environments. The present study tested whether significant inter-varietal variation exists for WUE in common bean (*Phaseolus vulgaris* L.) under well-watered and water-stressed conditions. Four varieties of common bean ('Cordoba', 'Nerina', 'Top Crop' and 'Wade') were grown in pots within a rainsheltered plant house. Two water treatments were imposed by maintaining plants at 75% (well-watered) and 45% (water-stressed) of field capacity (FC). Transpiration and biomass accumulation were measured by daily weighing and destructive sampling respectively. Biomass accumulation was linearly related to cumulative transpiration in all variety x water combinations. When averaged across all varieties, mean seasonal water use efficiency ( $WUE_m$ ) under water stress ( $4.025 \pm 0.102 \text{ gkg}^{-1}$ ) was significantly higher than under well-watered conditions ( $3.532 \pm 0.068 \text{ gkg}^{-1}$ ). Within a given water regime, there was significant inter-varietal variation of  $WUE_m$ . However, the ranking of varietal  $WUE_m$  differed with water regimes. 'Wade' had the highest  $WUE_m$  at 75% FC while 'Nerina' had the highest  $WUE_m$  at 45% FC. Periodic WUE ( $WUE_p$ ) was significantly higher during the initial 13-day period. Following a subsequent decline, a significant increase in  $WUE_p$  was observed during the pod-filling period.  $WUE_p$  had significant linear relationships with relative growth rate and net assimilation rate. However, no significant relationship was found between  $WUE_p$  and specific leaf area. It is recommended that the significant varietal variation in WUE present in common bean germplasm be used in breeding for drought tolerance. However, varietal screening should be done under both well-watered and water-stressed conditions to ensure a variety which would perform well under fluctuating seasonal environments.

**Key words:** Bean, *Phaseolus vulgaris*, water stress, water use efficiency.

**INTRODUCTION**

Common bean (*Phaseolus vulgaris* L.) is one of the most popular vegetable legumes in Sri Lanka.<sup>1</sup> It is grown across a range of agroecological zones where shortage of water is a major constraint to increase yields.<sup>2</sup> The relationship between crop yield and water use can be expressed as<sup>3</sup>:

Yield = Transpiration x Water use efficiency (WUE) x Harvest index  
 where WUE is the amount of biomass produced per unit of water transpired.

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As the scope to achieve a high level of transpiration (T) is limited in a drought-prone environment, increasing WUE offers an avenue for maintaining high yields under water stress.<sup>4</sup> However, conflicting evidence exists as to whether it is possible to increase WUE of a crop species through breeding and improved management.<sup>5-7</sup> Jones<sup>8</sup> showed that at the single leaf level, instantaneous WUE, defined as the ratio between photosynthesis and transpiration rates, is sensitive to a number of environmental and plant factors which influence stomatal conductance. However, at the crop (i.e. plant population) level, measurements of biomass production and transpiration over a longer period have shown remarkable constancy in WUE for a given species across varieties and a range of environments and management conditions.<sup>5</sup> Using the principles of gas exchange, Monteith<sup>6</sup> showed that WUE depends only upon the photosynthetic carboxylation pathway and the saturation vapour pressure deficit (D) between leaf and surrounding air. WUE was shown to be higher in C<sub>4</sub> species and to be inversely related to D. After a comprehensive review, Ludlow & Muchow<sup>7</sup> concluded that they were not aware of any proven differences in WUE within a species or within groups of C<sub>3</sub> or C<sub>4</sub> plants in the field. A major constraint in resolving the above conflict is the difficulty in measuring crop WUE in the field as it needs sophisticated instruments and financial resources.

However, interest in the search for inter-varietal variations in WUE has been renewed with the pioneering work of Farquhar *et al.*<sup>9</sup> on carbon isotope discrimination (D). Atmospheric CO<sub>2</sub> contains about 1.1% of the non-radioactive isotope <sup>13</sup>C. During photosynthesis, plants discriminate against the heavier <sup>13</sup>C in favour of <sup>12</sup>C. Consequently, the (<sup>13</sup>C/<sup>12</sup>C) ratio in plants is less than that in air. Therefore, D is defined as:

$$D = \frac{(^{13}\text{C}/^{12}\text{C})_{\text{air}}}{(^{13}\text{C}/^{12}\text{C})_{\text{plant}}} - 1$$

Farquhar and Richards<sup>10</sup> showed that D is inversely correlated with WUE, thus suggesting the possibility of a rapid screening method for WUE and drought tolerance. Wright *et al.*<sup>11</sup> observed varietal differences in D in groundnut which indicated variation in WUE. It was also shown that specific leaf area (SLA), i.e. leaf area per unit leaf biomass, was negatively correlated with WUE.

The present paper investigates the possible varietal variation of WUE in common bean and its response to water stress. As in the case of varietal variation, conflicting evidence exists on the effects of water stress on WUE. Water stress increases both stomatal ( $r_s$ ) and internal, mesophyll ( $r_i$ ) resistances thus affecting both photosynthesis and transpiration rates. The net effect of water stress on WUE is determined by the variation of ( $r_s/r_i$ ).<sup>11</sup> At the leaf level, there is evidence for both constant and increased WUE.<sup>11</sup> While Fischer &

Turner<sup>12</sup> and Ludlow & Muchow<sup>7</sup> have concluded that crop WUE in the field does not vary with water stress, Hebbar *et al.*<sup>13</sup> have reported significant increases in WUE under water stress.

Therefore, the objectives of the present experiments were to determine: (a) whether there are significant varietal variation in WUE of common bean; (b) whether WUE is significantly affected by water stress; (c) whether there is an interaction between varieties and water stress in their possible influence on WUE.

## METHODS AND MATERIALS

*Location:* The experiment was conducted from December, 1994 to February, 1995 in a plant house at the Faculty of Agriculture, University of Peradeniya. Four varieties of common bean (cv. Cordoba, Nerina, Topcrop and Wade) were grown in plastic pots (20 cm tall and 18 cm cross-sectional diameter) containing 3.8 kg of air-dried sandy-clay-loam soil.

*Experimental design:* The experimental treatment structure was a 4 x 2 factorial, with four varieties and two levels of soil water availability. The well-watered ( $W_1$ ) treatment was maintained at 75% of field capacity of the soil which was determined from initial measurements. The water-stressed ( $W_2$ ) treatment was maintained at 45% field capacity. This moderate level of water stress is representative of the stress levels experienced by most common bean crops grown in Sri Lanka (i.e. in the mid- and up-country intermediate zones). Common bean is known to have relatively poor drought tolerance as compared to other legumes<sup>14</sup> and therefore is not grown in areas subjected to severe water stress (i.e. dry zone).

The soil water contents that represent the above percentage points of field capacity were calculated. Accordingly, the total weight of the experimental pot (i.e. pot weight, soil and water) at each of the above water levels was determined for each pot. Pots were weighed daily and the required water levels were maintained by adding the amount of water lost through evapotranspiration during the period between successive weighings. The increase in plant weight due to growth during this short period was considered negligible when compared to the weight of water that passes through the soil-plant-atmosphere pathway.<sup>15</sup> The eight treatment combinations were laid out in a randomized complete block design with fifteen replicates.

*Crop management:* Two plants were grown in each pot. A mixture of top soil and compost was used as the potting medium. Basal fertilizer (267 mg/pot of urea, 329 mg/pot of triple super phosphate and 204 mg/pot of muriate of potash) was mixed into top soil at sowing. Top dressing (267 mg/pot of urea and 204 mg/pot

of muriate of potash) was applied at three weeks after planting. Plants were maintained free from pests and diseases by using appropriate plant protection measures.

The exposed soil surface in pots containing plants was covered with polythene to prevent soil evaporation. Five pots without plants were also maintained to monitor evaporation from the exposed soil surface.

*Measurements:* As described earlier, daily water loss through transpiration was measured by daily weighing to a resolution of 1 g. After adding the required amount of water to maintain the appropriate levels of water availability on a given day, the decrease in total pot weight on the subsequent day was taken as being predominantly due to transpiration. Biomass production was measured by destructive sampling at 13, 23, 36, 46 and 58 days after sowing (DAS). Six plants were harvested from each treatment on a given sampling date. Both roots and shoots were harvested. Dry weights were measured after oven drying at 80°C for at least 48 h.

*Water use efficiency:* For each treatment, WUE was calculated over a range of time scales. For a given treatment, a single value of WUE for the entire period of the experiment (0 - 58 DAS) was estimated by doing a simple linear regression between cumulative biomass and cumulative transpiration using data from all five samplings. The estimated slope of this relationship gives the WUE as defined by Passioura<sup>3</sup> and most other workers.<sup>4-7</sup> Significance of the differences between regression coefficients was tested by the method given in Snedecor & Cochran.<sup>16</sup>

WUE was also calculated for periods between successive samplings by computing the ratio between biomass increase and transpiration during each successive period. Significance of the differences in periodic WUE between different cultivars and water treatments were tested by analysis of variance (ANOVA).

*Relative Growth Rate (RGR) and Net Assimilation Rate (NAR):* RGR and NAR were calculated for each successive period between samplings by the following formulae<sup>17</sup>:

$$\begin{aligned} \text{RGR} &= (\log_e W_2 - \log_e W_1) / (t_2 - t_1) \\ \text{NAR} &= (W_2 - W_1) (\log_e L_2 - \log_e L_1) / (t_2 - t_1) (L_2 - L_1) \end{aligned}$$

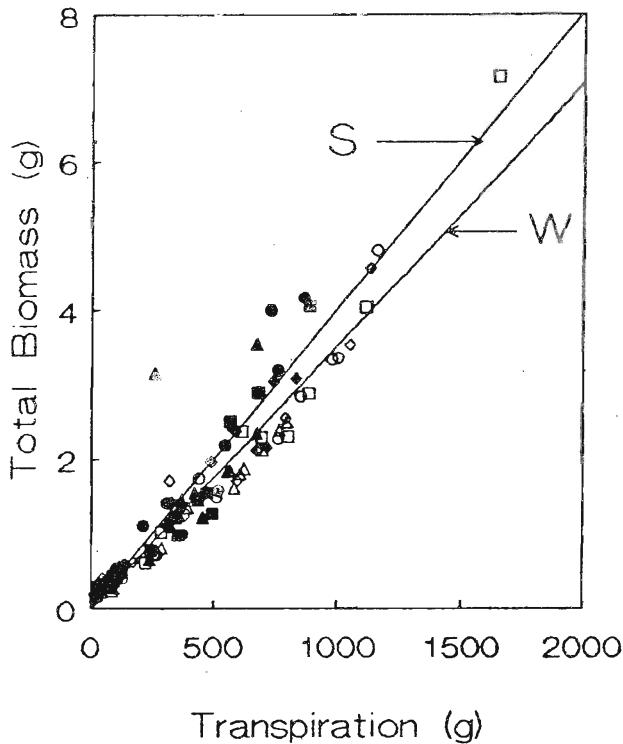
where,  $W_1$ ,  $L_1$ ,  $W_2$  and  $L_2$  are total dry weights and leaf areas per plant at times  $t_1$  and  $t_2$ . RGR measures the efficiency of the existing biomass in producing new biomass whereas NAR is a measure of the existing leaf area in producing new biomass. These indices of growth efficiency were computed to test whether they were significantly correlated with WUE.

*Specific Leaf Area (SLA)*: SLA at different sampling dates was calculated by obtaining the ratio between leaf area and leaf dry weight per plant. The arithmetic mean was taken as the mean SLA during the periods between successive samplings.<sup>18</sup> Subsequently, strength of the relationship between values of WUE and SLA for the corresponding periods was tested by correlation analysis.

## RESULTS

### Mean Water Use Efficiency. ( $WUE_m$ )

Biomass accumulation of all varieties over the entire growth period showed a significant linear relationship ( $R^2 > 90\%$ ) with cumulative transpiration under both well-watered and water-stressed conditions (Fig. 1).  $WUE_m$  of water-stressed plants ( $4.025 \pm 0.102 \text{ g kg}^{-1}$ ) was significantly higher than that of well-watered plants ( $3.532 \pm 0.068 \text{ g kg}^{-1}$ ) when averaged across all varieties. When analyzed individually, each variety showed a significant increase in  $WUE_m$  under water deficits (Table 1).



**Figure 1:** Relationship between cumulative transpiration (T) and biomass accumulation (W) of different varieties under two water regimes. Open symbols: well-watered treatment; Closed symbols: water-stressed treatment.  $\Delta$  Cordoba;  $\circ$  Nerina;  $\diamond$  Topcrop;  $\square$  Wade. Lines indicate regressions: Well-watered (W)-  $W = 3.532 (\pm 0.068) T$  ( $R^2 = 0.98$ ); Water-stressed (S)-  $W = 4.025 (\pm 0.102) T$  ( $R^2 = 0.94$ ).

Within each water treatment, there were significant ( $p < 0.05$ ) differences between the  $WUE_m$  of the different varieties tested (Table 1). However, relative performance of the different varieties was different under the two water regimes. Under well-watered conditions, the variety 'Wade' showed the highest  $WUE_m$  whereas under water-stressed conditions, 'Nerina' had the highest  $WUE_m$ . The variety 'Cordoba' which had the lowest  $WUE_m$  when the water supply was adequate showed significant increase in its  $WUE_m$  under water deficits. On the other hand, despite having the highest  $WUE_m$  in the higher water regime, 'Wade' showed a comparatively smaller increase in  $WUE_m$  under the lower water regime.

**Table 1: Mean seasonal water use efficiency ( $WUE_m$ ) of different common bean varieties under two water regimes.**

Variety	Well-watered		Water-stressed	
	$WUE \pm CL^*$ (g/kg)	$R^2$ (%)	$WUE \pm CL$ (g/kg)	$R^2$
Cordoba	$3.09 \pm 0.07$	99	$3.82 \pm 0.24$	95
Nerina	$3.53 \pm 0.11$	98	$4.43 \pm 0.22$	96
Topcrop	$3.51 \pm 0.14$	97	$3.81 \pm 0.12$	99
Wade	$3.76 \pm 0.14$	98	$3.99 \pm 0.20$	96
<i>Mean</i>	$3.53 \pm 0.07$	98	$4.03 \pm 0.10$	96

\* 95% Confidence Limits (CL) of the regression coefficients. Absence of overlap in confidence intervals indicate significant difference between regression coefficients.

### Periodic WUE ( $WUE_p$ )

All varieties showed significantly higher  $WUE_p$  (7.33-10.49 g kg<sup>-1</sup>) during the initial 13 day period in both water regimes (Fig. 2).  $WUE_p$  of all treatment combinations showed a decline (1.78-4.31 g kg<sup>-1</sup>) during the subsequent periods from 13-46 DAP. However, during the final period of measurement (46-58 DAP),  $WUE_p$  increased again in all treatments. Except for a few situations,  $WUE_p$  was greater under water-stressed conditions within a given variety during a given time period.

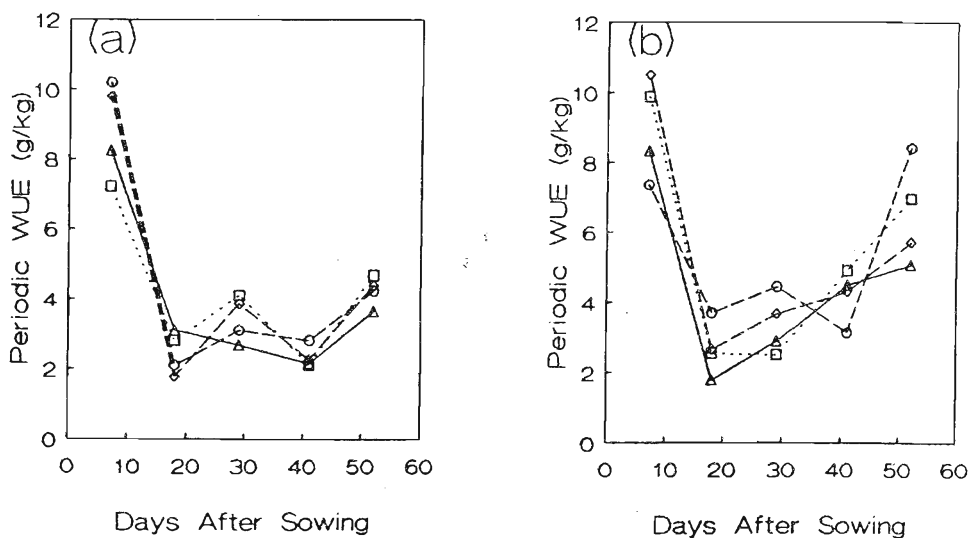


Figure 2: Variation of periodic WUE with time for different varieties under two water regimes. (a) well-watered; (b) water-stressed. Symbols are the same as in Fig. 1.

### Relationship between $WUE_p$ and Growth Parameters

There was a significant positive linear relationship ( $R^2 = 0.65$ ) between  $WUE_p$  and RGR (Figure 3) irrespective of the variety and water regime. The regression coefficients did not differ significantly ( $p=0.05$ ) between the two water regimes.

$WUE_p$  and NAR also showed a strong ( $R^2 = 0.83$ ) positive correlation for all varieties under both water regimes (Figure 4). There were no significant differences in regression coefficients between the two water regimes.

There was no significant correlation ( $R^2 = 0.09$ ) between  $WUE_p$  and SLA (Figure 5). The same was true for the two water regimes.

### Relationship between $WUE_m$ and Yield Parameters

The respective correlations between mean WUE and yield parameters at 58 DAS are shown in Figures 6 and 7.  $WUE_m$  was positively correlated with both pod yield and harvest index. However, the respective correlation coefficients of 0.22 and 0.31, indicate that correlations are not particularly strong.

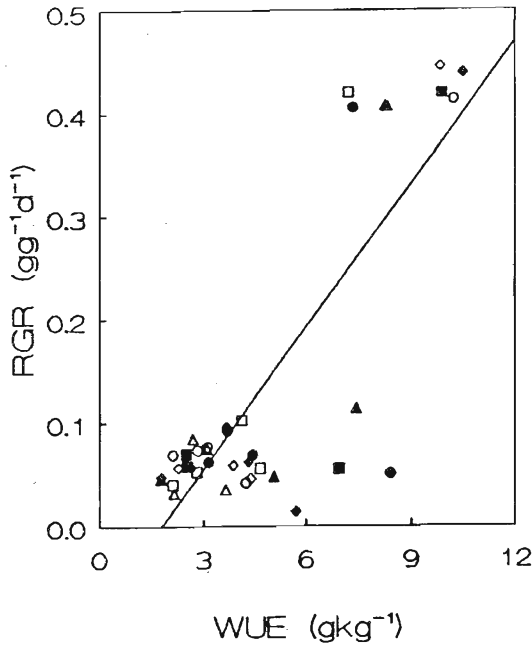


Figure 3: Relationship between RGR and WUE<sub>p</sub> for different varieties under two water regimes. Symbols are the same as in Fig. 1. Regression equation:  $RGR = -0.083 + 0.046 (WUE)$ . ( $R^2 = 0.65$ ).

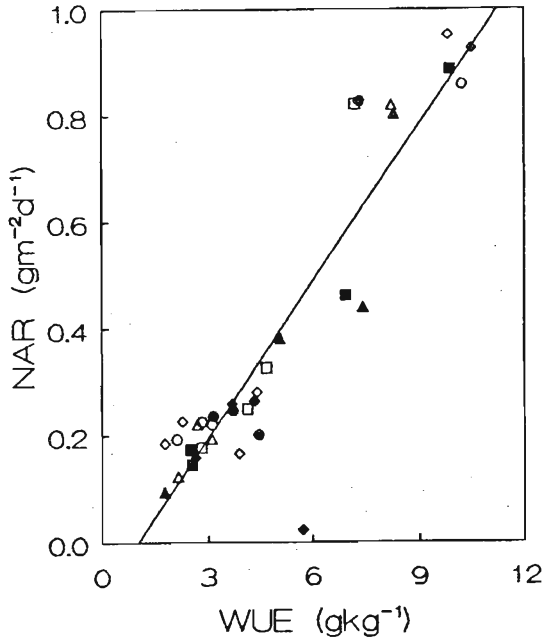


Figure 4: Relationship between NAR and WUE<sub>p</sub> for different varieties under two water regimes. Symbols are the same as in Fig. 1. Regression equation:  $NAR = -0.1 + 0.098 (WUE)$ . ( $R^2 = 0.83$ ).

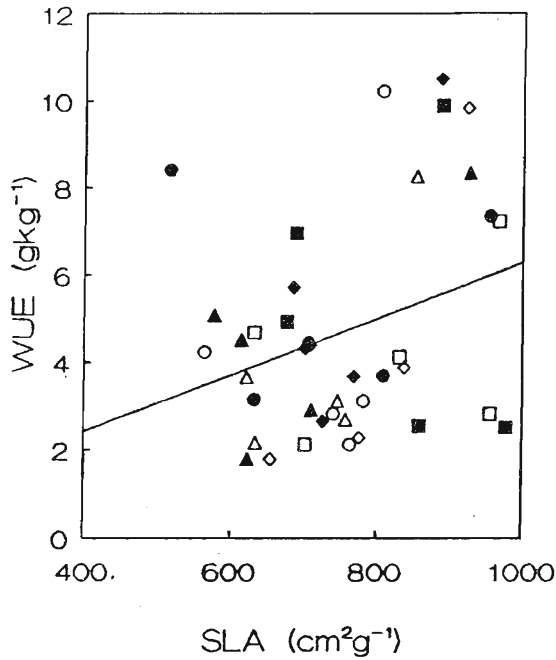


Figure 5: Relationship between  $WUE_p$  and SLA for different varieties under two water regimes. Symbols are the same as in Fig. 1. Regression equation:  $WUE = -0.14 + 0.0064 (SLA)$ . ( $R^2 = 0.06$ ).

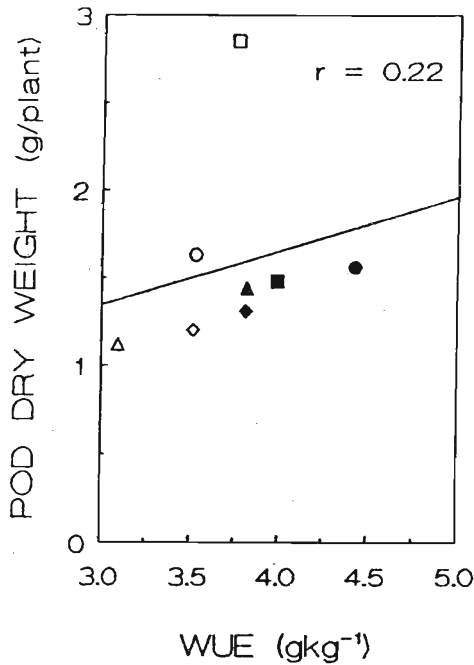


Figure 6: Relationship between  $WUE_m$  and pod yield at 58 DAS for different varieties under two water regimes. Symbols are the same as in Fig. 1.  $r$  = Correlation coefficient.

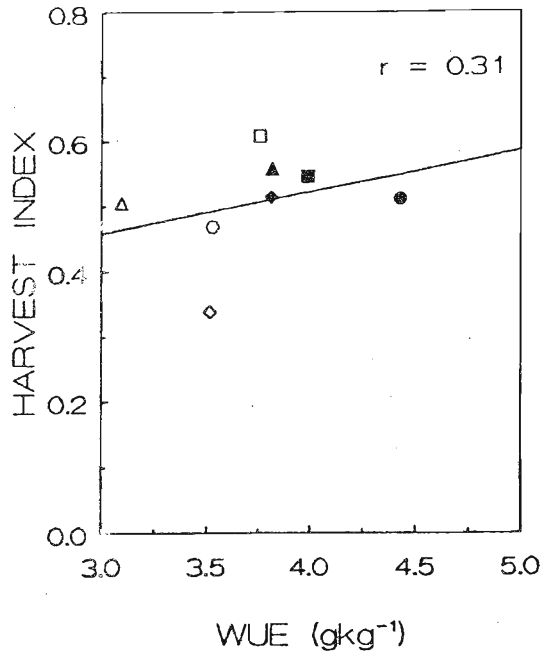


Figure 7: Relationship between  $WUE_m$  and harvest index at 58 DAS for different varieties under two water regimes. Symbols are the same as in Fig. 1.

## DISCUSSION

Results of this study showed that significant varietal variation in WUE exists within the common bean varieties grown in Sri Lanka. This variation could be utilized in screening germplasm for breeding varieties suited to field sites of varying water availability. However, some degree of caution has to be exercised in such a screening because of the differential performance of the varieties under different water regimes. A variety which may have a higher WUE under water-stress may not be the most superior one in terms of WUE under well-watered conditions and *vice versa*. Therefore, the variation of water availability, both within and between seasons, of a given site has to be considered in selecting germplasm on the basis of WUE. Although the present study was not specifically designed to measure pod yields, the positive correlations between WUE and pod yield and harvest index at 58 DAS adds weight to the significance of WUE as a useful selection criterion in breeding for high performance under drought.

The present work also confirmed the widely-held view that water stress increases the WUE in a given genotype.<sup>19</sup> This is most probably achieved by an increase in stomatal and mesophyll resistance.<sup>20,21</sup> However doubts have been raised as to whether this increased WUE under drought contributes significantly

to the final productivity. Jones<sup>19</sup> and Ludlow & Muchow<sup>7</sup> contend that final productivity is determined during the period when stomata are open and therefore when WUE is lower. Although WUE may be higher during the drought period, increased stomatal resistance would mean that the contribution to final biomass from this period may be small. Therefore, it may be advantageous to select varieties which have a higher ranking for WUE not only under drought but also under well-watered conditions. Among the limited number of varieties tested here, 'Nerina' and 'Wade' fulfil the above requirement.

Results of the present study provide important insights into the physiological basis of WUE. The significantly higher WUE levels during the initial period were probably due to lower maintenance respiratory losses in the smaller plants which were present at this stage. Since the increase in the total dry weight is due to the balance between photosynthesis and respiration, a lower respiration would increase the total biomass accumulated per unit of water transpired. The increase in  $WUE_p$  observed during the final period of measurement coincided with the flowering and pod formation period. The enhanced sink demand during this period probably caused a stimulation of the gross photosynthetic rate leading to an increase in  $WUE_p$ .

The linear relationships observed between  $WUE_p$  and growth efficiency parameters of conventional growth analysis (i.e. RGR and NAR) indicate that variations in photosynthetic efficiency rather than transpiration were the primary reason for the observed differences in  $WUE_p$ . The generality of this conclusion is confirmed by the absence of significant differences in the regression coefficients of these relationships across cultivars and water regimes. On the other hand, a higher transpiration when coupled with a higher WUE could achieve a significantly greater final biomass. The positive correlation between WUE and harvest index would ensure a higher pod yield. However, the physiological basis and underlying mechanisms of the above positive correlation have not been explained yet<sup>7</sup> and hence merit further investigation. The absence of a significant correlation between  $WUE_p$  and SLA agreed with the results observed by White *et al.*<sup>22</sup> for common bean. However, it contradicted with the results of Wright & Nageswara Rao<sup>22</sup> for groundnut.

Results of the present study have shown WUE to be a promising selection criterion when breeding for drought tolerance. However, two cautionary notes have to be mentioned. One is about the correlation between WUE and final productivity. Although, correlations were positive in the present study, there have been reports of negative correlations between productivity, in terms of pod yield, and WUE for some crop species including common bean.<sup>7, 19, 23</sup> The second cautionary note is about extrapolating results obtained in pot-grown single plants to plant populations growing in the field. Baldocchi,<sup>24</sup> Monteith<sup>6</sup> and Jones<sup>19</sup> have reported that the observed variations in WUE in single-plant

experiments may not always be reflected at crop level in the field. Differences in the degree of coupling to the surrounding atmosphere of single leaves and crop canopies<sup>19, 25</sup> which determines the change in transpiration per unit change in stomatal resistance could be the reason for the above observation. Therefore, the two issues noted above have to be resolved through further experimentation.

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