Water stress and water use efficiency in cowpea [Vigna unguiculata (L.) Walp.] under controlled environment

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Water use efficiency is one of the most important challenges for crop improvement programmes in the arid and semi-arid regions. An experiment was conducted from August to October 2011, in a plant house at Soil Research Institute, Kwadaso/Kumasi, in order to determine the effect of water stress on the vegetative stage of six cowpea varieties and assess agronomical mean for selecting water use efficient cowpea genotypes. A three replicated completely randomized design with two water treatments and six cowpea genotypes was used and data were collected on biomass (BM), water use (WU), water use efficiency (WUE), leaf senescence (LS) and root/shoot ratio (RSR). Highly significant effects of cowpea genotypes, water treatments and their interaction were observed on BM, WU, WUE and RSR. Water stress significantly decreased BM and WUE of water-stressed cowpea varieties compared to the control, and the largest reduction was observed in TN5-78 for BM (89%) and Nhyira for WUE (94%). The results also revealed that under water-stressed condition, varieties TN88-63 and Dan illa with relatively low WU, significantly recorded highest values of BM and WUE with 2.20 g and 4 g/kg, 1.78 g and 3g/kg respectively, while the largest percentage of 41.58% for RSR was recorded by variety TN5-78. BM showed a significant strong positive correlation (r = 0.96, p<0.001) with WUE, while a negative correlation was observed with RSR (r = -0.51, p<0.005). Also, a strong positive correlation (r= 0.97, p<0.001) was found between LS and R/S. The two varieties TN88-63 and Dan illa were found to be the most water use efficient cowpea cultivars.

Key words: Cowpea, water stress, water use efficiency, controlled environment.

INTRODUCTION

The arid and semi-arid zones of Africa are facing a massive challenge in agriculture as the climate changes, and improving the efficiency of water use by plants constitutes one of the most important challenges for crop breeders. Water-use efficiency (WUE) is defined as a ratio of biomass accumulation, expressed as carbon dioxide assimilation, total crop biomass, or crop grain yield, to water consumed, expressed as transpiration, evapotranspiration (ET), or total water input to the system (Sinclair et al., 1984). Transpiration efficiency (TE), referred to as intrinsic water use efficiency (Farquhar et al., 1989), can be evaluated at leaf level as the ratio of CO2 exchange rate to transpiration (Morgan et al., 1993) or the ratio of marketable yield or biomass produced to transpiration (Hattfield et al., 2001; Allison and Jones, 2005). However, Photosynthetic WUE is difficult to monitor over long periods. More conveniently and for agronomic assessment, WUE has been expressed as the ratio of biomass produced to water consumed, referred to as biomass WUE. Biomass WUE is known to be relatively constant for a given crop under a given climate and the prevailing air CO2 concentration (Hanks, 1983), regardless of whether water supply is ample or deficient (de Wit, 1958).

On the other hand, carbon isotope discrimination (Δ13C) was used to evaluate water use efficiency in crop plants and positive correlation between grain yields was found

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in wheat (Kirda et al., 1992; Condon and Richards, 1993; Araus et al., 1998). The positive correlation of grain yield with $\Delta^{13}C$ in several C$_3$ species (Merah et al., 2001; Monneveux et al., 2006) led to a positive correlation between $\Delta^{13}C$ and WUE under same water availability for all genotypes.

Contrary, Farquhar et al. (1982) demonstrated that according to the theory of C$_3$ plants, water use efficiency should be related to the extent that plants discriminate against the heavy stable isotope $^{13}C$ compared with the more abundant isotope $^{12}C$ ($\Delta$) in photosynthetic uptake of CO$_2$. Therefore $\Delta^{13}C$ and WUE should be negatively related. Since the first study on pot-grown broad wheat (Farquhar and Richards, 1984), there have been numerous studies which indicate that this negative association between $\Delta^{13}C$ and WUE is robust for plants of many C$_3$ species. An unexhaustive list of crop species for which this negative association has been found includes bread wheat (Condon et al., 1990; Ehdaie et al., 1991), barley (Hubick and Farquhar, 1989), peanut (Arachis spp.) (Hubick et al., 1986), common bean (Phaseolus vulgaris L.) (Ehleringer et al., 1991), cowpea (Vigna unguiculata L.) (Ismail and Hall, 1992), sunflower (Helianthus annuus L.) (Virgona et al., 1990), and chickpea (Cicer arietinum L.) (Udayakumar et al., 1998).

The theory proposed by Farquhar et al. (1982) relating $\Delta^{13}C$ to WUE is therefore well established at both the leaf and whole-plant levels. According to Hall et al. (1997), the value of this correlation to breeding is that $\Delta^{13}C$ can be measured on plants in the field nurseries, whereas WUE cannot. In principle, large numbers of genotypes could be evaluated, since it is simply necessary to take leaf samples (preferably at the same nodal position), dry them, and measure $\Delta^{13}C$ using an isotope mass spectrometer.

For cowpea, genotypic differences in $\Delta^{13}C$ have been described under field conditions (Hall et al., 1990, 1994). Unfortunately, both measurements in estimating WUE, ratio of CO$_2$ uptake to transpiration and carbon isotope discrimination had drawbacks. For the former, gas exchange measurements have not been effective in detecting genotypic differences in cowpea (Hall et al., 1992), while for the later, such measurements were expensive.

Most cowpea is produced in arid and semi-arid zones of Sub-Saharan Africa (SSA) where drought is a major production constraint due to low and erratic rainfall (Singh et al., 1997).

Focusing on the dire predictions of drought in several parts of SSA and increasingly scarce water resources, plant breeders must develop agronomic mean which maximizes crop production, such as the development of cowpea cultivars with moderate water use by selection for high water use efficiency.

Therefore, the main objective of this study is to determine the effect of water stress on the vegetative stage and assess agronomical mean for selecting water use efficient cowpea varieties.

**MATERIALS AND METHODS**

The experiment was conducted from August to October 2011, in a plant house at Soil Research Institute (Kwadaso) Kumasi/Ghana which is about 8 km away from the city of Kumasi. Temperature and relative humidity in the plant house measured were 28.6±2°C and 85.21±3%, respectively. Six cowpea varieties were used: Asontem and Nhyira were gotten from Crop Research Institute/Kumasi, while Dan Illa, IT9D-610, TN5-78 and TN88-63 were obtained from National Agricultural Research Institute of Niger (INRAN). Seeds of different genotypes were sown in pots (0.25 m diameter and 0.16 m height) filled with 7 kg silty loam and acidic (pH = 5.59) soil. Sowing was done on August 26th, 2011 at the rate of 3 seeds/pot and later thinned to one plant/pot seven days after planting (7 DAP). A total of thirty six pots (with drainage holes at the bottom) were used, out of which eighteen were irrigated at four days interval until ten days after planting (10 DAP), after which water was withdrawn. The remaining eighteen pots received water throughout the experiment (up to 35 DAP) and this served as the control. Experimental pots were arranged to obtain a planting distance of 50 cm × 25 cm. Five grams of SSP fertilizer (18% P$_2$O$_5$) was applied per pot by incorporating into the soil at planting. In order to ensure a clean pot, hand weeding was done first at one week after planting and subsequently when necessary.

Prior to every irrigation, each pot was weighed and the weight differences (kg) were converted to volume (ml). The values obtained for each pot represented the volume of water applied to that particular pot at that period. The average volume of the water used rate was determined for each genotype. The water use efficiency based on biomass was calculated according to Larcher (2003) as follows:

$$WUE\ (g/kg) = \frac{\text{Biomass (g/plant)}}{\text{Water used rate (kg/plant)}}$$

At harvest, the biomass and roots of each genotype in a replication were oven-dried at 72°C to a constant mass and their masses were taken with an electronic balance. Plants were scored for leaf senescence 17 days after planting on a scale of 0-10, dividing the percentage of estimated total leaf area that is dead by 10 as described by Bänziger et al. (2000), as follows:

1 = 10% dead leaf area  
2 = 20% dead leaf area  
3 = 30% dead leaf area  
4 = 40% dead leaf area  
5 = 50% dead leaf area  
6 = 60% dead leaf area  
7 = 70% dead leaf area  
8 = 80% dead leaf area  
9 = 90% dead leaf area  
10 = 100% dead leaf area

Data were subjected to ANOVA (Analysis of Variance)
Table 1. Effects of cowpea genotypes, water treatment and their interaction on biomass, water use and water use efficiency.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>G</td>
</tr>
<tr>
<td>Biomass (g)</td>
<td>0.56</td>
<td>10.12</td>
<td>4.47±3.60</td>
<td>*</td>
</tr>
<tr>
<td>Water use efficiency (g/kg)</td>
<td>0.97</td>
<td>35.25</td>
<td>13.08±12.3</td>
<td>*</td>
</tr>
<tr>
<td>Water use (g)</td>
<td>249</td>
<td>910</td>
<td>502.58±212</td>
<td>*</td>
</tr>
<tr>
<td>Root/shoot ratio (%)</td>
<td>8.75</td>
<td>42</td>
<td>20.42±8.11</td>
<td>*</td>
</tr>
<tr>
<td>Leaf senescence (%)</td>
<td>2.00</td>
<td>13.00</td>
<td>5.50±1.50</td>
<td>*</td>
</tr>
</tbody>
</table>

G = genotype; WT = water treatment; G × WT = interaction; * = significance at 1%, ± standard deviation; !! = measurement was made only on water-stressed cowpea genotypes.

Table 2. Mean effect of water stress on biomass, water use and water use efficiency of six cowpea varieties used in this study.

<table>
<thead>
<tr>
<th>Variety</th>
<th>BM (g)</th>
<th>WU (g)</th>
<th>WUE (g/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>WS</td>
<td>Ctrl</td>
<td>WS</td>
</tr>
<tr>
<td>Asontem</td>
<td>1.5±0.01</td>
<td>9.80±5</td>
<td>905±321</td>
</tr>
<tr>
<td>Dan illa</td>
<td>1.78±0.03</td>
<td>3.21±0.8</td>
<td>554±166</td>
</tr>
<tr>
<td>IT96D-610</td>
<td>1.31±0.01</td>
<td>7.81±4</td>
<td>800±257</td>
</tr>
<tr>
<td>Nhyira</td>
<td>1.1±0.01</td>
<td>9.18±4</td>
<td>675±220</td>
</tr>
<tr>
<td>TN5-78</td>
<td>0.57±0.01</td>
<td>5.09±3</td>
<td>621±157</td>
</tr>
<tr>
<td>TN88-63</td>
<td>2.22±0.01</td>
<td>9.99±4</td>
<td>580±105</td>
</tr>
<tr>
<td>LSD (0.05)</td>
<td>0.07</td>
<td>4.02</td>
<td>1.94</td>
</tr>
<tr>
<td>CV (%)</td>
<td>16</td>
<td>10</td>
<td>14</td>
</tr>
</tbody>
</table>

BM: biomass; WU: water use; WUE: water use efficiency; ± = standard deviation; CV = co-efficient of variation; WS = water stress; Ctrl = control.

RESULTS

At the plant house experiment, 25 days after imposing the water stress significant effects of genotypes, water treatments and their interaction were obtained on biomass (BM), water use (WU), water use efficiency (WUE), leaf senescence (LS) and RSR (Table 1).

Biomass

Highly significant differences (p<0.01) were observed for mean biomass subjected to water stress, in which the average mean ranged from 9.99 to 3.21 g for the control and from 2.20 to 0.57 g for the water-stressed varieties (Table 2). When compared to the control, the water-stressed cowpea genotypes showed significant differences. Only variety Dan illa under water-stressed condition showed continuous growth very much close to that of the control for the whole period of water stress. Under the water deficit, TN88-63 and Dan illa recorded the highest values of 2.20 and 1.78 g respectively, while the least value of 0.57 g was recorded by TN5-78. The same trend was observed under the control where Asontem was next to TN88-63 with biomass production of 9.80 and 9.99 g, respectively.

Water use and water use efficiency

Significant differences (p<0.001) were observed for water use and water use efficiency among cowpea varieties. It was deduced from Table 2 that the average water use efficiency ranged from 34 to 13 g/kg for the control and from 4 to 1 g/kg for the water-stressed varieties. The result indicated that there were significant differences (p<0.01) among the varieties for water use efficiency. All genotypes failed to show no significant differences between the water-stressed and control conditions. Under water-stressed condition, Dan illa and TN88-63 did not show any significant difference, while under the control, significant differences were observed among the varieties for water use efficiency. Under the control,
Nhyira recorded the highest value of 34 g/kg followed by Asontem (31 g/kg) for water use efficiency, while under the water-stressed condition TN88-63 and Dan illa with moderate water use (580 and 554 g respectively) recorded the highest values of 4 and 3 g/kg, respectively. The least value of 1 kg/g for water use efficiency was recorded by variety TN5-78 after twenty-five days of water stress.

### Leaf senescence

For leaf senescence, significant differences exist among cowpea varieties. Mean leaf senescence ranged from 6 to 2%. The highest value of 6% was recorded by TN5-78, while the least value of 2% was recorded equally by Asontem and IT96D-610 (Table 3).

### Root/shoot ratio

Mean percentage of root/shoot ratio ranged from 23.57 to 8.82% for the optimum condition, and from 41.58 to 17.47% for the water-stressed cowpea genotypes. Under the control, cowpea varieties were significantly different, while under the water-stressed condition, variety TN5-78 recorded the highest percentage (41.58%) of root/shoot ratio, which was significantly different from TN88-63 (26.86%), and also different from the other counterparts. The results in Table 3 indicated that variety Nhyira recorded the least percentage of root/shoot ratios of 20% under water-stressed condition.

### Correlations

In the plant house experiment, significant strong positive correlations (p<0.01) were found between biomass and water use efficiency (r = 0.96) (Figure 1A) and between leaf senescence and root/shoot ratio (r = 0.97) (Figure 2), while a negative relationship (r = -0.51) was found between biomass and root/shoot ratio (Figure 1B).

### DISCUSSION

**Biomass production**

In this study, water stress significantly reduced above ground biomass resulting in low biomass in severe water-stressed genotypes (25 days of water deficit). Relative reduction in biomass was more significantly (p<0.01) pronounced in TN5-78 and Nhyira, with 89 and 88% respectively, while the least relative reduction was recorded by Dan illa (45%) as compared with the control plants (Table 1). This agrees with observations made on other species (for example, maize, soybean, cotton and squash) where water stress led to stimulation of root growth and the suppression of shoot growth (Spollen et al., 1993), but does not agree with the results of Lewandowski and Clifton-Brown (2000) who reported that limiting water supply increased the proportion of shoot growth in all three different Miscanthus genotypes (M. x giganteus, M. sacchariflorus and M. sinensis). The result confirms the findings of Lu et al. (1999) while identifying the specific physiological mechanisms at the whole-plant and cellular levels responsible for drought resistance in barley. The authors reported that when subjected to -0.4 MPa root water deficit, the shoot growth in cv. Mona (on the basis of dry weight) decreased by 85.2%, as compared with the control plants, while the shoot growth in Wadi Qilt 23-39 was significantly less inhibited (74.8%) by the same root water deficit. The results obtained from TN5-78 and Nhyira suggested that the effect of drought was severe to reduce photosynthesis by decreasing leaf area and stem growth reducing ability of the crops to intercept solar radiation. This report is consistent with the findings of Prabhu and Shivaji (2000) who reported that the main effect of drought in the vegetative period was to reduce leaf, so that the crop intercepts less sunlight. The mechanisms underlying drought-tolerance strategy in Dan illa appeared to be related to the higher ability of osmotic adjustment because when plants are subjected to drought stress, a number of physiological responses

<table>
<thead>
<tr>
<th>Variety</th>
<th>Root/shoot ratio (%)</th>
<th>Leaf senescence (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>WS</td>
<td>Ctrl</td>
</tr>
<tr>
<td>Asontem</td>
<td>17.47±0.03</td>
<td>8.82±5.0</td>
</tr>
<tr>
<td>Dan illa</td>
<td>20.39±1.0</td>
<td>16.92±2.0</td>
</tr>
<tr>
<td>IT96D-610</td>
<td>20.31±0.04</td>
<td>23.57±2.0</td>
</tr>
<tr>
<td>Nhyira</td>
<td>20±0.3</td>
<td>18.09±1.0</td>
</tr>
<tr>
<td>TN5-78</td>
<td>41.58±0.4</td>
<td>10.18±17</td>
</tr>
<tr>
<td>TN88-63</td>
<td>26.86±0.3</td>
<td>20.84±3.0</td>
</tr>
<tr>
<td>LSD (0.05)</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td>CV (%)</td>
<td>4.10</td>
<td></td>
</tr>
</tbody>
</table>

± Standard deviation, CV = co-efficient of variation, WS = water stress, Ctrl = control.

#### Table 3. Mean effect of water stress on root/shoot ration and leaf senescence of the six cowpea varieties used in this study.
Figure 1. Relationship between biomass and root/shoot ratio (A) and biomass and water use efficiency (B).

were observed (Ludlow and Muchow, 1990; Fukai and Cooper, 1995). In some cultivated cereals, osmotic adjustment was found to be one of the most effective physiological mechanisms underlying plant tolerance to water deficit (Turner and Jones, 1980; Morgan, 1984; Blum, 1988; Zhu et al., 1997). Osmotic adjustment, as a process of active accumulation of compatible osmolytes in plant cells exposed to water deficit, may enable a continuation of leaf elongation, though at reduced rates (Turner, 1986).

Water use and water use efficiency

Cowpea under control recorded higher values of water use efficiency compared to their corresponding water-stressed genotypes. With regard to water use efficiency, variety TN88-63 which recorded the highest value of 4 g/kg, followed by Dan illa (3 g/kg) proved to be significantly more water use efficient varieties than the other counterparts. According to Blum (2005), this may be probably due to their ability to reduce their water use, which is reflected in higher water use efficiency, and is generally achieved by plant traits (for example, small plant size, small leaf area, reduced growth, etc.) and environmental responses that reduce yield potential. This result suggests that greater biomass production under water stress was associated with relatively low water use and greater water use efficiency as seen in TN88-63 and Dan illa. Values of water use efficiency based on biomass production of TN88-63, Dan illa and Asontem obtained
under water-stressed condition are quite similar to that of values found by Lewandowski and Clifton-Brown (2000) which ranged from 2.1 to 4.1 g DM kg\(^{-1}\) H\(_2\)O for \(M. x giganteus\) and \(M. sacchariflorus\), respectively (\(M. sinensis\) was intermediate) and the value for 2-year old \(M. x giganteus\) grown in large pots in a glasshouse (3.3 g DM kg\(^{-1}\) H\(_2\)O) (Jacks-Sterrenberg, 1995). Also, similar result was reported by Ogbonnaya et al. (2003) that high water use efficiency was recorded for TN 88-63 under water-stressed and well-watered conditions, respectively.

Both of these values of water use efficiency for cowpea varieties and \(Miscanthus\) grown in pots are much lower than the values reported recently by Beale et al. (1999) for an irrigated mature crop in the field (7.8 g DM kg\(^{-1}\) H\(_2\)O). This observation agrees with the findings of Cordon et al. (2002), who reported that under drier condition, the high water use efficient wheat genotype realized relatively a higher yield than the corresponding genotype with low water use efficiency. Conversely, at the well-watered site, the genotype experiencing higher water use efficiency realized a relatively poor yield, compared to the genotype with lower water use efficiency. The ability for crop plants to limit water use and transport, may be probably due to their osmotic adjustment within roots, because as soil water declines, it may provide an adaptive response to sustain root water uptake potentials to such an extent that the hydraulic driving force for water uptake and transport through the plant can be maintained (Turner and Jones, 1980). However, this value of osmotic adjustment has been challenged (Munns, 1998), particularly in relation to its suitability as a desirable trait in breeding programmes. He argues that genotypes expressing significant osmotic adjustment are likely to divert carbohydrates away from related processes, resulting in drought tolerance genotypes with low growth rates and poor biomass realization. In those cases, however where reduced water availability results in reduced rates of transpiration and sustained biomass accumulation, water use efficiency will be significantly increased. On the contrary, Munoz et al. (1998) documented that high yield potential and high yield under water-limited conditions are generally associated with reduced water use efficiency mainly because of high water use. Features linked to low yield potential, such as smaller plants (Martin et al., 1999) or short growth duration (Lopezcastaneda and Richards, 1994), ascribe high water use efficiency because they reduce water use.

**Leaf senescence and root/shoot ratio**

There was significant variation among cowpea varieties in the leaf duration under water-stressed condition. This variation among cowpea varieties may be probably due to the ability to maintain green leaf duration and high relative water content in water-limited condition as seen in Asontem and IT96D-610 (2%), compared to the sensitive variety TN5-78 with greater score for leaf senescence (6%). This result confirms previous results of numerous studies conducted in rainfed and irrigated conditions between the durum wheat and bread wheat varieties (Deumier, 1987; Gate et al., 1992; Mekliche, 1992). The lowest percentage of leaf senescence obtained from Asontem and IT96D-10 was probably due to the osmotic adjustment by accumulation of solutes such as sugars, or by a good regulation of the stomatal conductance. Also, Di Fozon et al. (2000) reported that genetic variation exists for foliar senescence and genotypes and plants with leaves which remain green for longer periods than normal are defined as “stay-green”.

Therefore, the present results suggest that the ‘stay
green’ mechanism in Asontem and IT96D-610 may be related to stomatal closure at low soil moisture content. Varieties Asontem, IT96D-610, Nhyira and Dan illa avoided water stress damage by reduced green leaf conductance and the utilization of water was optimized, while variety TN5-78 continued to function in spite of plant water deficit and lost green leaf area by senescence, which indicates a lack of adaptation to drought. But sometimes, the loss of green leaves at early onset of induced water stress may be adaptive to drought because crops plants use this strategy to intercept less solar radiation, so as to limit transpiration as seen in TN88-63.

On the other hand, drought stress significantly increased root/shoot ratio in cowpea varieties under water stress compared to the control. The lowest percentage for root/shoot ratio recorded by Nhyira, IT96D-610 and Dan illa may be probably explained by their ability to enhance root morphology and root growth which appears to be an important plant character for the adaptation of cowpea to water stressed-conditions. This result agrees with the finding of several authors who reported that an increase in root/shoot ratio of plants growing under water-stress environments was related to ABA content of roots and shoots (Sharp and LeNoble, 2002; Manivannan et al., 2007b). According to Fick et al. (1971), the water stress slows shoot growth more and sooner than it does root growth. But contrary, there was a decline in root/shoot ratio as seen for the three varieties (Nhyira, IT96D-610 and Dan illa), which implies that these varieties were able to maintain relatively their leaf area despite of water deficit. Also, the root growth was not significantly reduced under water deficits in maize and wheat (Sacks et al., 1997).

**Correlations**

Since dehydration, avoidance was achieved mainly by enhanced capture of the soil moisture (deep rooting system) and reduced transpiration via stomatal closure, the question was then whether these observations could lead to high water use efficiency in cowpea plants under water-limited environment. Under water-stressed condition, biomass, water use efficiency was indeed closely related with highly significant positive relationship (Figure 1B). The interpretation is that greater biomass was relatively associated with low water use (as seen in TN88-63 and Dan illa) and greater water use efficiency in one side and on the other side water deficit contributes to a significant reduction in leaf area, so as to reduce water loss through transpiration with immediate consequence of decreasing photosynthesis because the crop plant intercepts less radiation. Blum (2005) reported that for conditions where high water use efficiency (WUE) is an advantage because it is a marker for low water use, selection for the preferred plant type can be done by directly selecting for small plant size, small leaf area, or reduced growth duration rather than by using the more expensive selection criterion of water use efficiency (WUE) by way of carbon isotope discrimination. He also, reported that root/shoot dry matter ratio increases under drought stress, not because of an increase in root mass but due to a relatively greater decrease in shoot mass (Figure 1A). Similar results were also reported by Ogbonnaya et al. (2003), who found significant relationships between water use efficiency of cowpea in field conditions and root biomass, root volume, and shoot biomass in hydroponics.

**Conclusion**

It is clear from the results that genotypic variations exist among cowpea genotypes for water use efficiency, due to their relatively water use. The two varieties, TN88-63 and Dan illa, with the highest water use efficiency in this experiment are useful breeding materials for improving water use efficiency. However, Asontem and IT96D-610 with intermediate water use efficiency can be used as a source for developing delayed leaf senescence in cowpea breeding programme which is an important mechanism because it can enhance drought adaptation of early cowpea cultivars by enabling them to produce a greater second pod flush if the first flush is damaged by drought.

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