Physiological responses of chickpea genotypes to terminal drought in a Mediterranean-type environment

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Abstract

Two field experiments were carried out to investigate the effects of terminal drought on chickpea grown under water-limited conditions in the Mediterranean-climatic region of Western Australia. In the first experiment, five desi (small angular seeds) chickpeas and one kabuli (large round seeds) chickpea were grown in the field with and without irrigation after flowering. In the second experiment, two desi and two kabuli cultivars were grown in the field with either irrigation or under a rainout shelter during pod filling. Leaf water potential ($\Psi_l$), dry matter partitioning after pod set and yield components were measured in both experiments while growth before pod set, photosynthesis, pod water potential and leaf osmotic adjustment were measured in the first experiment only.

In the first experiment, total dry matter accumulation, water use, both in the pre- and post-podding phases, $\Psi_l$ and photosynthesis did not vary among genotypes. In the rainfed plants, $\Psi_l$ decreased below −3 MPa while photosynthesis decreased to about a tenth of its maximum at the start of seed filling. Osmotic adjustment varied significantly among genotypes. Although flowering commenced from about 100 days after sowing (DAS) in both experiments, pod set was delayed until 130–135 DAS in the first experiment, but started at 107 DAS in the second experiment. Water shortage reduced seed yield by 50 to 80%, due to a reduction in seed number and seed size. Apparent redistribution of stem and leaf dry matter during pod filling varied from 0 to 60% among genotypes, and suggests that this characteristic may be important for a high harvest index and seed yield in chickpea.

Keywords: Assimilate redistribution; Cicer arietinum (L.); Gas exchange; Osmotic adjustment; Water relations

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1. Introduction

Chickpea (Cicer arietinum L.) is grown across a wide range of environments, from the subtropics of India and north-eastern Australia to Mediterranean-climatic regions around the Mediterranean basin and in southern Australia (Siddique et al., 1999). It has become an important pulse crop in Australia over the past decade. In subtropical areas it is sown after the summer monsoonal rains and grows on stored soil moisture. In Mediterranean-climatic regions it is sown in autumn or spring and grows during the cool wet months of winter and spring. In both environments chickpea crops are exposed to drought during pod set and seed filling (terminal drought). Additionally, the crops can be exposed to low temperatures at flowering that inhibit pod set (Lawlor et al., 1998; Srinivasan et al., 1999) and high temperatures during seed filling that limit yields (Buddenhagen and Richards, 1988). While chickpea is considered one of the most drought-tolerant of the cool season food legumes, the basis of its tolerance is unknown (Singh, 1993).

Methodologies for a better understanding of yield improvement under drought conditions have been reviewed recently (Turner, 1997). Leaf water potential represents an easy measure of water deficit and leaf gas exchange may provide a good 'sensor' of the stress. Production of dry matter, early vigour, phenological plasticity and osmotic adjustment have been identified as some of the key characteristics for improved yield and yield maintenance under drought (Turner, 1997). In the present study, these characteristics were studied on six genotypes of chickpea grown on a fine-textured, commercial Group N Bradyrhizobium immediately before sowing. The plots received 72 kg/ha of triple superphosphate drilled with the seed at sowing. Broad-leaved and grass weeds were controlled by conventional methods. Native budworm (Helicoverpa spp.) was controlled using insecticides. A 5 m section at one end of each plot was trickle irrigated commencing at flowering (108 DAS) and ending just before maturity. Irrigation equivalent to pan evaporation occurred twice weekly, corresponding to 152 mm of water applied over a 64 day period. Minimum and maximum air temperatures, rainfall and incident total
solar radiation were recorded on a daily basis using an automatic weather station at the site.

2.1.3. Water potential and photosynthesis
The leaf water potential ($\Psi_l$) of upper (unshaded) expanded leaves and the water potential of pods ($\Psi_p$) 20 to 25 days after setting were measured around midday (10:30 to 14:30 h) on clear sunny days (photosynthetically active radiation above 1700 µmol m$^{-2}$ s$^{-1}$) at approximately weekly intervals between 95 DAS and 174 DAS using the pressure chamber technique as described previously (Leport et al., 1998). At the same time and on similar leaves to those used for measurements of leaf water potential, the rate of net photosynthesis was measured with a portable, open gas exchange system (Model LCA3, ADC, Hoddesdon, UK) as described previously (Leport et al., 1998). All measurements of water potential and photosynthesis were replicated three times per plot and per date of measurement, using a different plant for each measurement.

2.1.4. Osmotic adjustment
At 129, 144 and 164 DAS, upper fully expanded leaves were sampled and immediately frozen for osmotic potential measurements while the closest leaf on the same plant was collected in a plastic bag for the measurement of relative water content (Turner, 1981). Osmotic potential was measured on expressed sap on the thawed samples by vapour pressure osmometry using Wescor (Wescor Inc., Logan, UT, USA) C-52 sample chambers and a Wescor HR-33T dew-point microvoltmeter (Turner, 1981). The osmotic potential at full turgor ($\pi_{100}$) was calculated as:

$$\pi_{100} = \pi \times \text{RWC}$$

where RWC is the relative water content and $\pi$ the measured osmotic potential at that RWC. A single measurement of $\pi$ and RWC was made per plot and per date of measurement. The level of osmotic adjustment was estimated from the difference in $\pi_{100}$ between leaves from the rainfed and irrigated plants.

2.1.5. Green area and dry matter partitioning
Plant samples (0.5 m$^2$ quadrat) from the rainfed end of each plot were harvested at ground level on 46, 72, 101, 115, 129, 143, 156, 171 DAS and at maturity (186 DAS for Kaniva, 178 DAS for the other genotypes). Any leaf material on the ground was collected and added to the sample. Border rows were not harvested to avoid edge effects. Plant samples were dried to constant weight and weighed. A 0.5 m length of crop was left between sampling areas to minimize edge effects on the adjacent sampling area. A subsample of three (129 and 143 DAS), four (115, 156 and 171 DAS), five (101 DAS), six (46 and 72 DAS), and 10 uniform plants (at maturity) was also collected from the plot adjacent to the quadrat cuts. These subsamples were partitioned into leaves, stems, flowers, and pods, and, at maturity, seeds for dry matter determination. Green area was determined on the leaf, stem and pod components (projected area only) using a Li-Cor LI-3100 (Li-Cor Inc., NE, USA) area meter. The green area/shoot dry weight ratios of the sample plants and the dry weights of the bulk plant cuts were used to calculate the green area index. Instantaneous spot measurements of the fraction of incident solar radiation intercepted by the canopy near solar noon were obtained from incident photosynthetically active radiation 0.5 m above and below the canopy with a 0.9 m long linear quantum sensor (Li-Cor Inc., NE, USA). At the same time that dry matter samples were taken, soil water content was measured at 20 cm intervals from 10 cm to 170 cm depths in the soil by the neutron scattering technique using a Model 503DR CPN (California Nuclear Pacific, CA, USA) moisture meter.

2.1.6. Yield components
Yield components were determined on both the irrigated and rainfed plants at maturity. Harvest index was calculated at maturity as the ratio of seed dry weight to total above-ground crop dry weight. The total number of pods (which included all fertile and infertile pods), number of seeds (which included all seeds above 20 mg) and seed weights were measured on each of 10 plants, and from these measurements the number of pods and
seeds per plant, number of seeds per pod and mean seed weight were calculated. Seed and pod number per square metre were calculated from the number of pods (or seeds) per plant and the ratio of dry matter per unit area and per plant.

In the rainfed chickpeas, the start of flowering and start of podding were recorded, corresponding to when 50% of plants had at least one fully open flower with visible corolla coloration, and at least one visible pod (3 mm), respectively.

2.2. Experiment 2

2.2.1. Trial design

Four chickpea genotypes, including two desi types, cv. Tyson (121 mg seed\(^{-1}\)), the newly-released cultivar Sona (220 mg seed\(^{-1}\)), a sister line of acc. ICCV88201 used in Experiment 1 (Section 2.1.1), and two kabuli types, cv. Kaniva (422 mg seed\(^{-1}\)), and the newly-released cultivar Bumper (470 mg seed\(^{-1}\)), obtained from a desi by kabuli cross, were grown in 1997 in a deep yellow sand (Quartzipsamment) with pH 6.0 to 6.5, at CSIRO Floreat Park, Perth, Western Australia. The soil was spatially and vertically uniform. The crops were grown in two blocks, one of them positioned so it could be automatically covered by a rainout shelter during rainfall events, and each block was fully randomized with three replicates of each chickpea genotype.

2.2.2. Management

The plants were sown at a depth of 5 cm on 18 June 1997 in plots 3 m wide (17 rows, 16 cm apart) and 4 m long (size of each block 12 m \(\times\) 12 m) at a seeding rate that gave established plant populations of 30–38 plants m\(^{-2}\). All seeds were inoculated with a commercial Group N Bradyrhizobium immediately before sowing. The plots received 120 kg/ha of superphosphate two weeks prior to sowing, and 50 kg/ha of a commercial mixed fertilizer (corresponding to 6.0 kg/ha of N, 2.6 kg/ha of P, 7.1 kg/ha of K, 3.5 kg/ha of S, and 1.8 kg/ha of Ca) six and 10 weeks after sowing. Weeds were controlled chemically. Both blocks were trickle irrigated commencing at flowering (94 DAS). In the block outside the rainout shelter, irrigation was maintained until the plants under the rainout shelter reached physiological maturity (131 DAS). In the block under the rainout shelter, irrigation was stopped at pod set (107 DAS), and thereafter the rainout shelter was positioned automatically over the crop during each rainfall event. Irrigation occurred every two days, corresponding to 44 mm of water applied over a 15 day period in the block under the rainout shelter and to 149 mm of water applied over a 39 day period in the irrigated block outside the rainout shelter. Rainfall was recorded on a daily basis using a manual rain gauge at the site. Minimum and maximum air temperatures were recorded on a daily basis using a data logger Testostor175 (Testo Gmbh & Co., Lenzkirch, Germany).

2.2.3. Water potential

\(\Psi_f\) was measured 107, 113, 118, 119, 120, 124, 127 and 131 DAS, following the same procedure as in Experiment 1 (Section 2.1.3).

2.2.4. Dry matter partitioning

Plant samples from both blocks (hereafter referred to as the water stressed and irrigated treatments) were harvested weekly at ground level from beginning of pod set (107 DAS) to maturity (138 DAS for the water stressed desi cultivars, 141 DAS for the water stressed Kaniva cultivar, 145 DAS for the water stressed Bumper cultivar, and 159 DAS for the irrigated plants). 10 plants were collected for the first four harvests, and 20 plants at maturity. Any leaf material on the ground was collected and added to the sample. Subsamples, corresponding to three plants out of the 10, or six out of the 20, were partitioned into leaves, stems, pod walls and seeds for dry weight determination. All plant samples were dried to constant weight and weighed. Dry matter per unit area was calculated from the measured dry matter per plant and the measured plant density for the corresponding plot.

2.2.5. Yield components

Yield components, start of flowering and start of podding were determined in both irrigated and water stressed plants, following the same procedure as in Experiment 1 (Section 2.1.6).
2.3. Statistical analysis

Means and standard errors were calculated with the SAS (SAS Institute, 1987) MEANS procedure and tests for differences among genotypes and treatments were performed using a one-way and a two-way ANOVA (SAS general linear model procedure). Significantly different species ($P > 0.05$) were identified with the LSD test. Correlations were derived using the SAS CORR SPEARMAN procedure.

3. Results

3.1. Experiment 1

3.1.1. Seasonal conditions

In 1995 at Merredin, daily maximum air temperatures were around 16°C from sowing to 100 DAS, around 19°C for the next 45 days and around 25°C from hereafter until maturity [Fig. 1(A)]. Daily minimum air temperatures below 0°C were observed on five occasions near the onset of flowering [Fig. 1(A)]. Until 153 DAS, daily minimum air temperatures were never above 10°C for more than two consecutive days and then after 153 DAS rose to above 13°C. Daily total solar radiation was around 10 MJ m$^{-2}$ at sowing and increased steadily to a maximum of 28 MJ m$^{-2}$ at 183 DAS (Fig. 1B). Including 60 mm just before sowing, growing season rainfall (May–November) was 313 mm [Fig. 1(C)], 86 mm more than the long-term average. Before pod set commenced 275 mm fell, but plants received only 38 mm during pod development, including 28 mm on 159 DAS.

3.1.2. Water potential and photosynthesis

For both irrigated and rainfed plants, no consistently significant differences were observed among genotypes in either midday leaf water potential or midday pod water potential (Fig. 2). In the irrigated plants the midday leaf water potential ($\Psi_l$) was between $-0.5$ and $-1.0$ MPa before pod development and between $-1.0$ and $-1.9$ MPa after pod initiation, while in the rainfed plants $\Psi_l$ decreased to $-3.6$ MPa after pod initiation and recovered to about $-2.0$ MPa after the 28 mm of rainfall on 159 DAS. The midday pod water potential ($\Psi_p$) was always 0.2 to 0.4 MPa above $\Psi_l$, except in rainfed plants after the rainfall event on 159 DAS when $\Psi_p$ and $\Psi_l$ were similar (Fig. 2).

The mean photosynthetic rate of the irrigated plants, except at 151 and 167 DAS, ranged from 21 to 27 μmol m$^{-2}$ s$^{-1}$ in all genotypes (Fig. 2). The decrease of the rate of net photosynthesis in irrigated plants at 151 and 167 DAS coincided with very windy conditions during measurement. In the rainfed plants, the rate of net photosynthesis decreased rapidly to values of 2 to 2.5 μmol m$^{-2}$ s$^{-1}$ after 124 DAS. The decrease in photosynthetic rate coincided with the initiation of pod set. In the rainfed plants, the recovery in $\Phi_p$ after rainfall on 159 DAS had no effect on the rate of leaf photosynthesis. By 159 DAS, only 13% of the leaves were still green in the rainfed Tyson, 20 to 26% in the other rainfed desi chickpea, and...
38% in the rainfed Kaniva. By 174 DAS, all leaves were senescent in the rainfed desi plants, while 9% of leaves were still green in the rainfed Kaniva.

3.1.3. Osmotic adjustment

Osmotic adjustment, in those genotypes in which it occurred, was maximal at 145 DAS (Fig. 3) by which time leaf photosynthesis was already low (Fig. 2). No osmotic adjustment was observed in the kabuli chickpea Kaniva or in the desi chickpea T1069. Osmotic adjustment was largest in CTS60543 (1.3 MPa), and intermediate (0.4 to 0.9 MPa) in Tyson, T1587 and ICCV88201.

3.1.4. Crop growth

Flowering commenced on 100 DAS for CTS60543, 103 DAS for T1069, and 106 to 108 DAS for the four other genotypes. The first pods were observed four weeks later, on 130 DAS in all desi genotypes including the cold tolerant selection CTS60543, and 135 DAS in the kabuli genotype (Fig. 2). The above-ground total dry matter in the irrigated plants at maturity was about 1000 g m$^{-2}$ and only significantly lower in Tyson than in the other genotypes (Table 1); in the rainfed chickpeas the dry matter was about 60 to 70% of that in the irrigated plants (Table 1). In the rainfed plots, all genotypes achieved their maximum dry weight at 143 DAS, and then decreased by 10 to 30% in the four desi genotypes [Fig. 4(A)].

Dry matter was significantly higher in Kaniva than in the desi genotypes at 72 and 101 DAS, but after 143 DAS it decreased markedly so that there was no significant difference at maturity. In addition to the loss of total dry matter there was also some apparent redistribution of dry matter during pod filling. Table 2 shows the decrease of stem plus leaf dry matter between maximum accumulation and maturity for the rainfed plots. During seed filling there was a reduction in leaf plus stem dry matter in all desi
Table 1

Above-ground dry matter (g m$^{-2}$), seed yield (g m$^{-2}$), harvest index, pod (PN) and seed numbers (SN), and seed weights (SW) at maturity of six genotypes of chickpea grown under irrigated and rainfed conditions at Merredin, Western Australia, in 1995 (Experiment 1a)

<table>
<thead>
<tr>
<th></th>
<th>Tyson</th>
<th>ICCV88201</th>
<th>T1587</th>
<th>T1069</th>
<th>CTS60543</th>
<th>Kaniva</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry matter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Irrigated</td>
<td>819b</td>
<td>1056a</td>
<td>1049a</td>
<td>1010a</td>
<td>1033a</td>
<td>980ab</td>
</tr>
<tr>
<td>Seed yield</td>
<td>351bc</td>
<td>368abc</td>
<td>42ka</td>
<td>1010b</td>
<td>405ab</td>
<td>303c</td>
</tr>
<tr>
<td>HI</td>
<td>0.43a</td>
<td>0.35bc</td>
<td>0.41ab</td>
<td>0.38bc</td>
<td>0.39b</td>
<td>0.31d</td>
</tr>
<tr>
<td>PN (m$^{-2}$)</td>
<td>221ab</td>
<td>1854ab</td>
<td>2203ab</td>
<td>1802b</td>
<td>223ab</td>
<td>280ab</td>
</tr>
<tr>
<td>SN (m$^{-2}$)</td>
<td>1.3a</td>
<td>1.2bc</td>
<td>1.2c</td>
<td>1.2bc</td>
<td>1.3ab</td>
<td>0.6d</td>
</tr>
<tr>
<td>SW (mg)</td>
<td>12bc</td>
<td>1955b</td>
<td>176c</td>
<td>198bc</td>
<td>155d</td>
<td>414a</td>
</tr>
<tr>
<td>Rainfed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry matter</td>
<td>522a</td>
<td>613a</td>
<td>585a</td>
<td>639a</td>
<td>607a</td>
<td>659a</td>
</tr>
<tr>
<td>Seed yield</td>
<td>204ab</td>
<td>194ab</td>
<td>200ab</td>
<td>221a</td>
<td>209ab</td>
<td>163b</td>
</tr>
<tr>
<td>HI</td>
<td>0.39a</td>
<td>0.32b</td>
<td>0.34b</td>
<td>0.35ab</td>
<td>0.34b</td>
<td>0.25c</td>
</tr>
<tr>
<td>PN (m$^{-2}$)</td>
<td>154ab</td>
<td>1130bc</td>
<td>123ab</td>
<td>1135c</td>
<td>145ab</td>
<td>52d</td>
</tr>
<tr>
<td>SN (m$^{-2}$)</td>
<td>191bc</td>
<td>1230bc</td>
<td>136bc</td>
<td>123ab</td>
<td>172ab</td>
<td>496d</td>
</tr>
<tr>
<td>SN (pod$^{-1}$)</td>
<td>1.2a</td>
<td>1.1bc</td>
<td>1.1bc</td>
<td>1.1c</td>
<td>1.2ab</td>
<td>0.9d</td>
</tr>
<tr>
<td>SW (mg)</td>
<td>102d</td>
<td>118b</td>
<td>142bc</td>
<td>149b</td>
<td>123d</td>
<td>317a</td>
</tr>
</tbody>
</table>

* A separate ANOVA was performed for each parameter and for irrigated and rainfed plants. Values with the same letter within a row are not significantly different (P>0.05).

3.1.6. Yield components

Under irrigated conditions, the highest seed yield was observed in T1587 while Kaniva had the lowest yield (Table 1). The harvest index (HI) in the irrigated Kaniva was significantly lower than in the desi genotypes. In the rainfed chickpeas, seed yields were about half (range 42–53%) of the yields in the irrigated plants. In the rainfed plants, HI was lowest in Kaniva and highest in Tyson. In the irrigated plants, Kaniva had a significantly lower number of pods per unit area than the desi chickpeas (Table 1). The proportion of PAR intercepted by plants was greater than 85% in all genotypes.

3.1.5. Water use

There was little variation among the genotypes in total water use, in water use before pod initiation and in water use after podding (Table 3). The profile of water use with depth did not show any significant differences among genotypes; 90% of the water was extracted from the upper 80 cm of the soil (data not shown).
Table 3

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Water use (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
</tr>
<tr>
<td>Tyson</td>
<td>268ab</td>
</tr>
<tr>
<td>ICCV88201</td>
<td>250b</td>
</tr>
<tr>
<td>T1587</td>
<td>274a</td>
</tr>
<tr>
<td>T1069</td>
<td>269ab</td>
</tr>
<tr>
<td>CTS60543</td>
<td>257ab</td>
</tr>
<tr>
<td>Kaniva</td>
<td>262ab</td>
</tr>
</tbody>
</table>

A separate ANOVA was performed for each measurement of water use. Values with the same letter within a column are not significantly different (P > 0.05).

The expense of seed numbers which were reduced in genotypes with large seeds. Despite the water shortage during seed filling, the weight per seed was only reduced by 19 to 25% in all genotypes (Table 1).

3.2. Experiment 2

In 1997, the daily minimum and maximum air temperatures in Perth were 7 to 10 °C warmer than those recorded in 1995 at Merredin. The total amount of rainfall from sowing date to maturity was 337 mm, including 309 mm before pod set. In addition crops received 51 mm through irrigation before pod set. After pod set commenced, the fully irrigated plants received 126 mm of water, including 98 mm through irrigation and 28 mm of rainfall (i.e. total rainfall and irrigation = 486 mm). The plants under the rainout shelter did not receive any irrigation or rainfall after pod set (i.e. total rainfall and irrigation = 360 mm).

The Vpd of both the irrigated and water stressed plants was similar to those obtained in Experiment 1, with no significant differences among genotypes. Values of Vpd were between −0.6 and −0.8 MPa during pod development in the irrigated plants and decreased rapidly between 107 and 118 DAS to values of −2.8 to −3.1 MPa in the stressed plants (data not shown).

Flowering commenced at almost the same time as in Experiment 1 (94 to 98 DAS), but pods

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**Table 2**

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Leaf+stem dry matter (% of maximum)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tyson</td>
<td>56c</td>
</tr>
<tr>
<td>ICCV88201</td>
<td>27b</td>
</tr>
<tr>
<td>T1587</td>
<td>36b</td>
</tr>
<tr>
<td>T1069</td>
<td>36b</td>
</tr>
<tr>
<td>CTS60543</td>
<td>38b</td>
</tr>
<tr>
<td>Kaniva</td>
<td>4a</td>
</tr>
</tbody>
</table>

*Values with the same letter are not significantly different (P > 0.05).*

ICCV88201 and T1069 which were half the size of the kabuli seeds, in both irrigated and rainfed conditions. The increase in seed size was at the expense of seed numbers which were reduced in genotypes with large seeds. Despite the water shortage during seed filling, the weight per seed was only reduced by 19 to 25% in all genotypes (Table 1).
Table 4

Above-ground dry matter (g m$^{-2}$), seed yield (g m$^{-2}$), and harvest index (HI) at maturity of four cultivars of chickpea grown under irrigated and water stressed conditions at Perth, Western Australia, in 1997 (Experiment 2)*

<table>
<thead>
<tr>
<th></th>
<th>Tyson</th>
<th>Sona</th>
<th>Kaniva</th>
<th>Bumper</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Irrigated</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry matter</td>
<td>496a</td>
<td>494a</td>
<td>561a</td>
<td>524a</td>
</tr>
<tr>
<td>Seed yield</td>
<td>233a</td>
<td>184a</td>
<td>113b</td>
<td>71c</td>
</tr>
<tr>
<td>HI</td>
<td>0.47a</td>
<td>0.37a</td>
<td>0.20b</td>
<td>0.14b</td>
</tr>
<tr>
<td><strong>Water stressed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry matter</td>
<td>159b</td>
<td>241ab</td>
<td>259ab</td>
<td>327a</td>
</tr>
<tr>
<td>Seed yield</td>
<td>50b</td>
<td>69a</td>
<td>26c</td>
<td>30c</td>
</tr>
<tr>
<td>HI</td>
<td>0.31a</td>
<td>0.29a</td>
<td>0.10b</td>
<td>0.09b</td>
</tr>
</tbody>
</table>

* A separate ANOVA was performed for each parameter and pod set) in four water stressed chickpea cultivars grown at Perth, Western Australia, in 1997 (Experiment 2).

Fig. 5. Change with time in the leaf and stem dry weight (ratio of dry weight at the day of measurement versus dry weight at pod set) of four water stressed chickpea cultivars grown at Perth, Western Australia, in 1997 (Experiment 2).

4. Discussion

One major limitation of chickpea in the cool Mediterranean climate of the south-western Australian cropping zone is its inability to avoid terminal drought by flowering earlier and setting pods at low temperatures. At Merredin, in 1995 we observed some variation among the genotypes in the time to flowering, especially in CTS60543. This putatively cold tolerant line (Lawlor et al., 1998) started flowering one week before Tyson, but did not set pods earlier than the other genotypes. Possibly the day temperatures below 15 °C observed during the four weeks after flowering in 1995 were too cold for pod set in any genotype.

In the irrigated plots in Experiment 2, the seed yields of all four cultivars were lower than those in the rainfed plots of Experiment 1, while the HI in Tyson and in Sona were slightly higher than in irrigated Tyson and ICCV888201 (a sister line of Sona) of Experiment 1, respectively (Table 4). The pod and seed number per square metre, and seed size characteristics in the irrigated plants were similar to those observed in the rainfed plots in Experiment 1 (data not shown).
et al., 1982; Leport et al., 1998). With the development of water deficits, the rate of photosynthesis in the rainfed treatment decreased linearly with \( \psi_l \) at a mean rate of about 6 \( \mu \text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1} \) in all six genotypes. This differs from the response reported previously for chickpea in which photosynthesis decreased markedly at a \( \psi_l \) of \(-0.8 \) to \(-0.9 \) MPa (Leport et al., 1998). The reason for the difference in response between seasons is not clear, but may reflect the more gradual development of water deficits in 1995. Nevertheless, while 1995 was a season with above average rainfall, leaf photosynthesis had decreased to 10% of its maximum rate (i.e. 2.5 to 2 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) in all genotypes by the time that seed filling began, as in chickpea in 1994 which was a season with below average rainfall.

The higher water potential in the pods (\( \psi_p \)) than in the leaves (\( \psi_l \)), may be associated with the position of the pod in the shade of the leaves, and also to the lower density of stomata on the pods. We were not able to measure any significant carbon dioxide exchange in pods in either the rainfed or irrigated plants (data not shown). The gas exchange of the pod is not considered to be a significant source of assimilate for seed development in chickpea (Saxena and Sheldrake, 1980; Sheoran et al., 1987). However, in field pea, CO\(_2\) respired by the seeds is released inside the pod, where its concentration is very high (Atkins and Pate, 1977), and the pod wall is assumed to play a significant role in the reassimilation of respired CO\(_2\) (Flinn et al., 1977). While leaf photosynthesis decreased with the decrease of \( \psi_l \), we do not know whether the pod wall was able to recycle respired CO\(_2\) as \( \psi_p \) decreased.

Osmotic adjustment has been reported in chickpea when subjected to drought (Morgan et al., 1991; Ruggiero et al., 1991; Leport et al., 1998). Our data indicated that there was considerable genetic variation from 0 to 1.3 MPa in osmotic adjustment among the six chickpea genotypes, but that it only occurred at low values of leaf water potential and when the rates of photosynthesis were already low (at 145 DAS). Thus, in contrast to other results on cool season pulses (Subbarao et al., 1995), osmotic adjustment was not associated with the maintenance of high levels of leaf photosynthetic activity, but it may have helped to maintain the low but positive rates of leaf photosynthesis at low water potential.

In a comparison across a wide range of pulses growing under water-limited conditions, Thomson and Siddique (1997), Thomson et al. (1997), Leport et al. (1998) and Siddique et al. (1999) showed that seed yield was correlated with early dry matter production. This has led Siddique et al. (1993) to suggest that the seed yield of pulses may be increased in low rainfall areas of Western Australia by selecting species with high dry matter production. In the two experiments in this study the amount of dry matter produced was influenced by the timing of the onset of water deficits. When the data for desi chickpea collected over several sites and seasons were compared, it is clear that the initial rate of dry matter production was similar in all cases (Fig. 7), but the maximum amount of dry matter produced was determined by the commencement of water shortage. As chickpea has an indeterminate growth habit, the initiation of a water deficit induced by low rainfall or termination of irrigation not only determines the maximum dry matter production, but also the number of pods and seeds that are set. It is therefore not surprising that the number of pods or seeds per unit area is correlated with the total dry matter (\( r^2 = 0.83 \) for pod number, \( r^2 = 0.92 \) for seed number, \( P < 0.01 \)) and the time to the onset of...
Wery et al. (1993) has suggested that the translocation of reserves in chickpeas is already very high and higher than in faba bean, lentil and field pea. However, the data on dry matter partitioning during seed filling in this study shows that the apparent redistribution of reserves in chickpea is highly variable (0–60\% ) and suggests that redistribution of assimilates is a characteristic that may be improved through breeding and selection. In the desi chickpea Tyson, preliminary data indicated that the decrease in the stem dry weight corresponded to a drastic decrease in storage carbohydrates from 30 to 3\% of stem dry weight, (Itani, personal communication). It is clear that our data on dry matter partitioning does not take into account the variations of the synthesis of structural biomass versus remobilisation. Indeed, in the second experiment where the stress occurred much more rapidly than in the first, it was not possible to show any remobilisation while variations in dry matter seems to show a greater ability to maintain water deficits (\( r^2 = 0.70 \) for pod number, \( r^2 = 0.85 \) for seed number, \( P < 0.01 \)).

However, high dry matter production does not necessarily translate into high seed yields, when we compare different genotypes. In 1995, Kaniva produced the highest dry matter, but had a significantly lower seed yield than the desi genotypes under rainfed conditions (Table 1). Our data indicate that in addition to dry matter accumulation before the commencement of pod set, partitioning into seeds and the ability of the plants to redistribute reserves from stems and/or leaves are likely to be necessary for high yield. While changes in dry matter alone do not definitively indicate redistribution of assimilates, the data in the first experiment suggest that dry matter was redistributed during seed filling from above-ground vegetative plant parts in the desi chickpeas. By contrast, the kabuli chickpeas had the highest maximum above-ground dry matter in both Merredin and Perth, but were the genotypes with the lowest apparent redistribution of dry matter from the leaves and stems and the lowest yields. In the desi types that showed an apparent redistribution of up to 60\% of dry matter, the decrease in dry matter was almost equal from leaves and stems (data not shown). Redistribution may also occur from the pod wall of rainfed chickpea, as demonstrated by Davies et al. (1999). Wery et al. (1993) has suggested that the translocation of reserves in chickpeas is already very high and higher than in faba bean, lentil and field pea. However, the data on dry matter partitioning during seed filling in this study shows that the apparent redistribution of reserves in chickpea is highly variable (0–60\% ) and suggests that redistribution of assimilates is a characteristic that may be improved through breeding and selection. In the desi chickpea Tyson, preliminary data indicated that the decrease in the stem dry weight corresponded to a drastic decrease in storage carbohydrates from 30 to 3\% of stem dry weight, (Itani, personal communication). It is clear that our data on dry matter partitioning does not take into account the variations of the synthesis of structural biomass versus remobilisation. Indeed, in the second experiment where the stress occurred much more rapidly than in the first, it was not possible to show any remobilisation while variations in dry matter seems to show a greater ability to maintain structural biomass production in the kabuli chickpea Kaniva than in the desi type Tyson. Nevertheless, the comparison of dry matter in the second experiment still classified the genotypes in the same way as in the first experiment. Indeed, the introduction of desi characteristics into Bumper (a kabuli by desi cross) may be responsible for the greater ability to redirect its photosynthesised products toward the seeds rather than into the vegetative part in this cultivar than in Kaniva and may indicate the potential for improving the assimilate redistribution in kabuli chickpea. Further, as the redistribution is likely an important component of seed yield in chickpea, harvest index should be strongly associated with seed yield. In both experiments, our data indicated that HI was closely correlated with seed yield (\( r^2 = 0.87, P < 0.01 \)) and with the apparent redistribution of dry matter from leaves and stems in the rainfed plots in 1995 (\( r^2 = 0.98, P < 0.01 \)).

Fig. 7 highlights a problem with evaluating drought resistance in indeterminate species. In determinate cereals, drought resistance is evaluated as yield under drought compared to potential yield obtained under adequately watered conditions. In indeterminate species, irrigation is usually stopped...
when plants in the water-limited plot reach physiological maturity. In Experiment 2, the irrigation was stopped in the irrigated treatment when the water stressed plants were at physiological maturity at 130 DAS. This was when water shortage started in the field at Merredin in Experiment 1. As a consequence, dry matter production, seed yield and yield components in the irrigated plants in Experiment 2 were very similar to those found under rainfed conditions in Experiment 1. However, the water stressed plants had markedly reduced total above-ground dry matter, seed number, seed yield and harvest index, giving a relative yield under drought [expressed as a percentage of yield potential (Fischer and Maurer, 1978)] of about 60% in 1995, 20–30% in 1994 and 1997, but only 14% in 1994 and 1997 if the 1995 irrigated plants were used to give the yield potential. Thus in indeterminate species such as chickpea it is difficult to compare the drought resistance across sites and seasons, as its evaluation may simply reflect the length of time that irrigation is maintained in the plots used to determine potential yield.

5. Conclusions

There were no consistent differences in water potential and leaf photosynthesis among the genotypes of chickpea exposed to terminal drought. At Merredin, none of the six genotypes studied were able to avoid drought by early pod development. Although some genotypes flowered earlier than others, all genotypes began pod set at the same time due to the failure of flowers to set pods in the cool spring temperatures. As a consequence, at Merredin, where cold temperatures did not allow early pod set, there was only a poor correlation between high seed yield and early growth or maximum dry matter production in the chickpea genotypes studied. However, our data show that a high HI is necessary for a high yield and that partitioning and redistribution of dry matter from stems and leaves is apparently one of the main characteristics resulting in high seed yield in chickpeas growing under Mediterranean-type conditions. Verification of this using labelled carbon is warranted.

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References

Atkins, C.A., Pate, J.S., 1977. An IRGA technique to measure CO₂ content of small volumes of gas from the internal atmospheres of plant organs. Photosynthetica 11, 214–216.
Adaptation to water-deficit in chickpea breeding lines by osmoregulation: relationship to grain-yields in the field. Field Crops Res. 27, 61–70.