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European Journal of Agronomy 11 (1999) 279–291

European Journal of Agronomy

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

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Accepted 19 July 1999

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 (Ψ_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, Ψ_l and photosynthesis did not vary among genotypes. In the rainfed plants, Ψ_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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1161-0301/99/$ – see front matter
PII: S1161-0301(99)00039-8

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, neutral-to-alkaline soil in the Mediterranean-climatic region of Australia. The genotypes used were a desi (small angular seeds) cultivar, Tyson, a kabuli (large round seeds) cultivar, Kaniva, and four desi advanced breeding lines, which had 14 to 30% higher yields than cv Tyson in 1994, a season with below average rainfall (Siddique, personal communication). The aim of the study was to identify the morphological and physiological characteristics of chickpea that may affect yields in these low rainfall environments. As dry matter redistribution was identified as a key characteristic under terminal drought, this was more intensively studied in a second experiment. In this second study two desi cultivars, Tyson and Sona, and two kabuli cultivars, Kaniva and Bumper, were studied to determine whether there was any variation among genotypes for assimilate redistribution.

2. Materials and methods

2.1. Experiment 1

2.1.1. Trial design

Six chickpea (*Cicer arietinum* L.) genotypes, including five desi types: cv. Tyson (121 mg seed^{-1}), acc. ICCV88201 (194 mg seed^{-1}), acc. T1587 (165 mg seed^{-1}), acc. T1069 (182 mg seed^{-1}), and acc. CTS60543 (158 mg seed^{-1}) and one kabuli type: cv. Kaniva (422 mg seed^{-1}) were grown in 1995 on a red brown earth (Calcic Haploxeralf) with a neutral surface pH (6.2 to 6.9) and pH increasing with depth to 8.6 (Thomson et al., 1997) at Merredin (31°30′ S, 118°12′ E), Western Australia. The trial was a randomized block design with four replicates of each chickpea genotype, and with a buffer plot (chickpea, cv. Dooen) at each end of the trial.

2.1.2. Management

The plants were sown at a depth of 5 cm on 13 May 1995 in plots 1.44 m wide (eight rows, 18 cm apart) and 30 m long at a seeding rate that gave established plant populations of 32–37 plants m^{-2}. All seeds were inoculated with a commercial Group N *Bradyrhizobium* immediately before sowing. The plots received 72 kg/ha of triple superphosphate drilled with the seed at sowing. Broad-leafed 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 (Ψ_l) of upper (unshaded) expanded leaves and the water potential of pods (Ψ_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 (π_{100}) was calculated as:

$$\pi_{100} = \pi \mathrm{RWC}$$

where RWC is the relative water content and π the measured osmotic potential at that RWC. A single measurement of π and RWC was made per plot and per date of measurement. The level of osmotic adjustment was estimated from the difference in π_{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 × 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

Ψ_1 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. 1(B)]. 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 (Ψ_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 Ψ_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 (Ψ_p) was always 0.2 to 0.4 MPa above Ψ_l, except in rainfed plants after the rainfall event on 159 DAS when Ψ_l and Ψ_p were similar (Fig. 2).

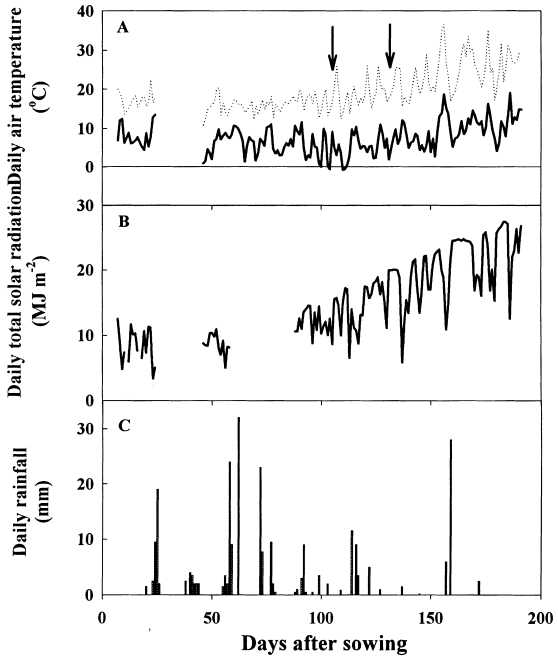

Fig. 1. (A) Daily minimum (—) and maximum (…) air temperatures. (B) Daily incident solar radiation. (C) Daily rainfall during the growing season at Merredin, Western Australia, in 1995 (Experiment 1). The arrows denote the mean date of first flower (first arrow) and first pod (second arrow) in the rainfed chickpeas. The gaps between 25 and 45 DAS (A and B), and between 59 and 87 DAS (B) correspond to missing data.

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 Ψ_l 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

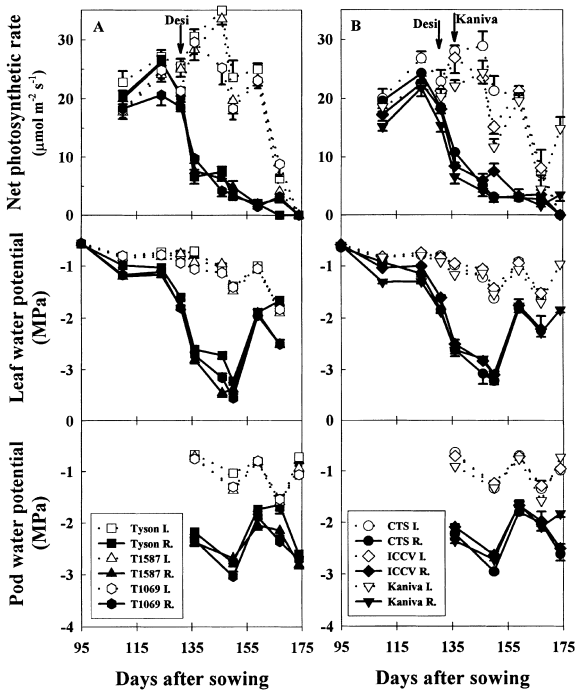

Fig. 2. Change with time in the midday leaf net photosynthetic rate, leaf and pod water potential of six irrigated (open symbols) and six rainfed (closed symbols) chickpea genotypes grown in the field at Merredin, Western Australia, in 1995 (Experiment 1). The six genotypes are separated into two groups (A and B) for clarity. The arrows denote the date of first pod in the rainfed chickpeas. Bars = ± one standard error of the mean when larger than the symbol.

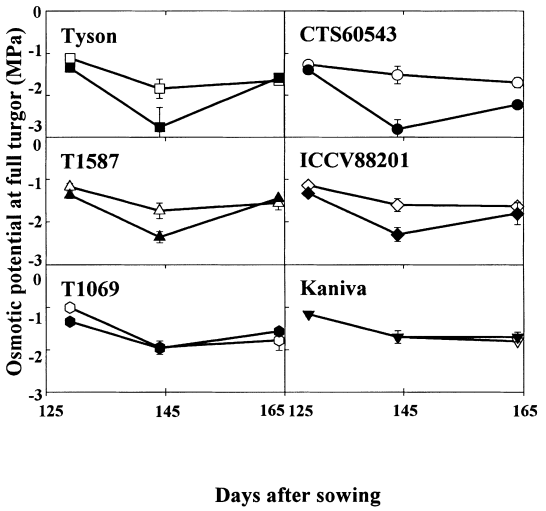

Fig. 3. Change with time of the calculated leaf osmotic potential at full turgor (π_{100}) in six irrigated (open symbols) and six rainfed (closed symbols) chickpea genotypes grown in the field at Merredin, Western Australia, in 1995 (Experiment 1). Bars = ± one standard error of the mean ($n=4$) when larger than the symbol.

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 1)[a]

	Tyson	ICCV88201	T1587	T1069	CTS60543	Kaniva
Irrigated						
Dry matter	819b	1056a	1049a	1010a	1033a	980ab
Seed yield	351bc	369abc	428a	384ab	405ab	303c
HI	0.43a	0.35bc	0.41ab	0.38bc	0.39b	0.31d
PN (m^{-2})	2211ab	1854ab	2203ab	1802b	2233a	943c
SN (m^{-2})	2933a	2183abc	2555abc	2129a	2830ab	787bc
SN (pod^{-1})	1.3a	1.2bc	1.2c	1.2bc	1.3ab	0.8d
SW (mg)	129e	195b	176c	194bc	155d	416a
Rainfed						
Dry matter	522a	613a	585a	639a	607a	659a
Seed yield	204ab	194ab	200ab	221a	209ab	163b
HI	0.39a	0.32b	0.34b	0.35ab	0.34b	0.25c
PN (m^{-2})	1549a	1158bc	1238abc	1135c	1453ab	523d
SN (m^{-2})	1918a	1230c	1381bc	1224c	1726ab	496d
SN (pod^{-1})	1.2a	1.1c	1.1bc	1.1c	1.2ab	0.9d
SW (mg)	102d	158b	142bc	145b	123cd	317a

[a] 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 ($P>0.05$).

genotypes from 27% in ICCV88201 to almost 60% in Tyson, with no significant reduction in Kaniva.

In the rainfed plots, the green area index reached a maximum earlier than the maximum dry matter [Fig. 4(B)]. The maximum green area index was around 5.0 in Kaniva, 4.6 in CTS60543 and about 4.0 in the other desi chickpeas. The higher leaf area in Kaniva was reflected in a greater interception of incident photosynthetically-active radiation (PAR) at 72 to 115 DAS [Fig. 4(C)]. From 115 to 143 DAS 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).

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). In the rainfed plots, all genotypes had 27 to 45% fewer pods per square metre compared to the irrigated plots. The desi chickpeas had 20 to 30% of double-seeded pods (1.2 to 1.3 seeds per pod), while Kaniva had 10 to 20% empty pods (0.8 to 0.9 seeds per pod) and these were not affected by the terminal drought. The largest seeds occurred in Kaniva and the smallest seeds occurred in Tyson, which had seeds only one third the size of those in Kaniva, in both irrigated and rainfed conditions (Table 1). The largest seeds in the desi chickpeas were found in

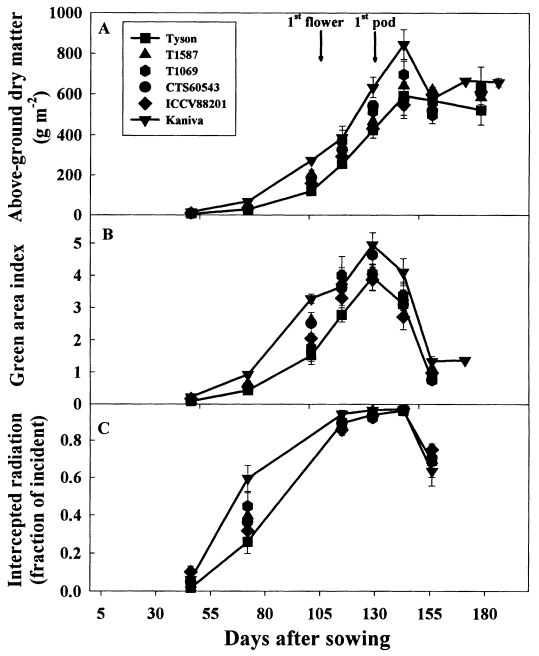

Fig. 4. Change with time in (A) above-ground dry matter, (B) green area index, and (C) interception of photosynthetically active radiation in six rainfed chickpea genotypes grown in the field at Merredin, Western Australia, in 1995 (Experiment 1). The data points for Tyson and Kaniva are joined for clarity. The arrows denote the mean date of first flower (first arrow) and first pod (second arrow) in the rainfed chickpeas. Bars = ±one standard error of the mean ($n=4$) when larger than the symbol.

Table 2
Reduction in leaf plus stem dry matter during seed filling as a fraction of maximum dry weight for six chickpea genotypes grown under rainfed conditions in the field at Merredin, Western Australia, in 1995 (Experiment 1)[a]

Genotype	Δleaf + stem dry matter (% of maximum)
Tyson	58c
ICCV88201	27b
T1587	36b
T1069	36b
CTS60543	38b
Kaniva	4a

[a] 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 3
Total, pre- and post-podding water use (mm) for six chickpea genotypes grown under rainfed conditions in the field at Merredin, Western Australia, in 1995 (Experiment 1)[a]

Genotype	Water use		
	Total	Pre-podding	Post-podding
Tyson	268ab	234ab	34ab
ICCV88201	250b	216b	34ab
T1587	274a	234ab	40a
T1069	269ab	235ab	34ab
CTS60543	257ab	229ab	28ab
Kaniva	262ab	239a	23b

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

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 Ψ_1 of both the irrigated and water stressed plants was similar to those obtained in Experiment 1, with no significant differences among genotypes. Values of Ψ_1 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

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)[a]

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

[a] 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 ($P>0.05$).

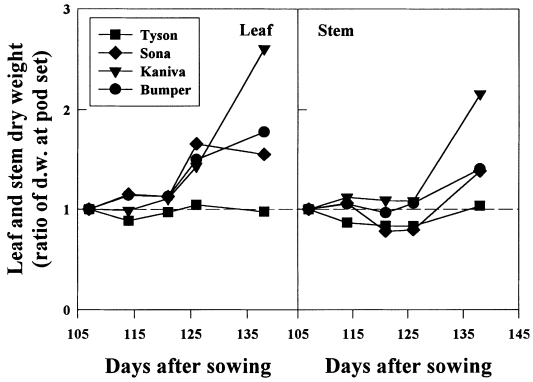

Fig. 5. Change with time in the leaf and stem dry weight (ratio of dry weight at the day of measurement versus dry weight at pod set) in four water stressed chickpea cultivars grown at Perth, Western Australia, in 1997 (Experiment 2).

began setting around 30 days earlier (102 to 106 DAS). Dry matter partitioning was measured only from beginning of pod set (107 DAS) until maturity. Dry matter production was approximately half that in Experiment 1 in both the irrigated and water stressed plants (Table 4). There were no significant differences among the four genotypes in the maximum amount of dry matter in the irrigated plants. The maximum dry matter produced in the water stressed plants was about half that in the irrigated and was significantly lower in Tyson and significantly higher in Bumper (Table 4). In the irrigated plants, the stem and pod dry matter of all genotypes and the leaf dry matter of the kabuli lines increased in all genotypes until maturity at 159 DAS, the leaf dry matter in the desi lines did not change significantly after 126 DAS (data not shown). In the water stressed plants, there was no variation in stem and leaf dry matter during pod development in Tyson compared with the start of pod set, a slight increase in Sona and Bumper stem dry matter, and more consistent increase in Kaniva (Fig. 5).

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 ICCV88201 (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).

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 (Savithri et al., 1980; Srinivasan et al., 1999). By contrast, in Perth, where the minimum and maximum air temperatures were warmer, there was minimal delay between flowering and pod set in all four cultivars.

When no water deficit occurred, the average rate of net leaf photosynthesis was high and only small differences were observed among the six genotypes. The values observed were consistent with previous measurements on chickpea (Singh

et al., 1982; Leport et al., 1998). With the development of water deficits, the rate of photosynthesis in the rainfed treatment decreased linearly with Ψ_l at a mean rate of about 6 μmol m^{-2} s^{-1} MPa^{-1} in all six genotypes (Fig. 6). This differs from the response reported previously for chickpea in which photosynthesis decreased markedly at a Ψ_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 μmol m^{-2} 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 (Ψ_p) than in the leaves (Ψ_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 Ψ_l, we do not know whether the pod wall was able to recycle respired CO_2 as Ψ_p decreased.

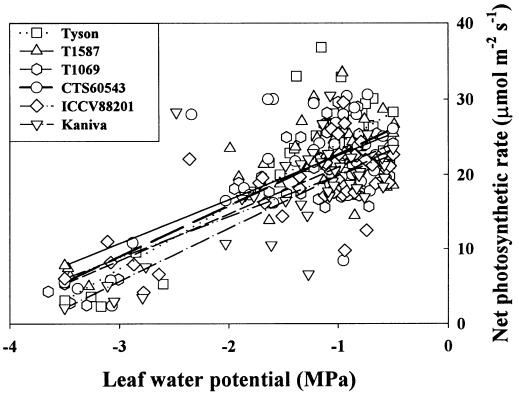

Fig. 6. Relationship between midday leaf net photosynthetic rate and midday leaf water potential in six chickpea genotypes grown in the field at Merredin, Western Australia, in 1995 (Experiment 1).

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

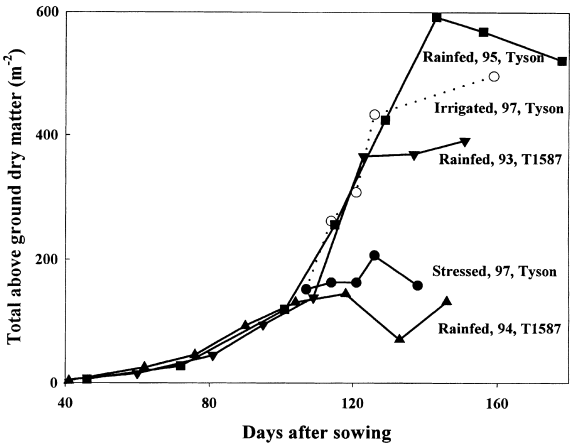

Fig. 7. Change with time in the above-ground dry matter in chickpea grown at Perth under fully irrigated and water stressed conditions in 1997 (Experiment 2, cv. Tyson), and in the field at Merredin under rainfed conditions in 1995 (Experiment 1, cv. Tyson), in 1994 (Leport et al., 1998, cv. T1587) and in 1993 (Thomson et al., 1997, cv. T1587).

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 photosynthetised 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.

Acknowledgements

We thank J.S. Malden, for dry matter sampling and collection of weather data, C.A. Toynes and I.F. LeCoultre, L. Maiolo and L. French, for assistance with the measurements at the field site, and L. Young for the day-to-day running of the experiment. We are grateful to Dr. B.D. Thomson for his helpful advice on the conduct of the experiment at Merredin, Dr. R.J.N. Emery for his help with statistical analyses, and Drs. M. Dracup and S.P. Loss for their useful comments on the manuscript. This research was supported by the Cooperative Research Centre for Legumes in Mediterranean Agriculture.

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